Systematic Zoology

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Systematic Zoology

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Symposium: Subspecies and Clines

THIS symposium entitled "The Subspecies versus the Cline: Their Biological and Nomenclatural Significance," was arranged for the Society of Systematic Zoology by James A. Peters. J. Speed Rogers presided over its presentation at the annual meeting of the Society in Boston on December 30, 1953.

Introduction

JAMES A. PETERS

THE primary object of this symposium was the exchange of ideas concerning infraspecific categories among representatives of the various fields of systematic research. The title "The Subspecies versus the Cline" was chosen to concentrate the discussion on these two types of infraspecific variation, and should not be construed as a suggestion of antagonism between them. It has become more and more obvious in recent years, however, that the subspecies no longer holds a sacrosanct place in systematic thought, and that the time has arrived for an evaluation of its current status.

When the various speakers were approached with reference to their participation, it was suggested that each concern himself with current methods of handling the question of clinal variation as a biological as well as a taxonomic problem in his particular field of specialization. It was felt that systematists in general could benefit by a summary of the status of the cline in as many fields as it was feasible to include. Infraspecific variation is not the special domain of any one field of interest, but is common ground to all systematists. Obviously, however, it is difficult for a specialist in one field to keep up with developments in each of the many divisions of systematics. The symposium was designed to bring the whole up to date concerning the activities of its parts.

It was felt desirable to inquire into the biological significance of clinal variation to settle the question of its universal application. Since universality could not be tested with only a few fields represented on the symposium, the fields were chosen on the basis of the likelihood of this problem's having arisen. This happens only after workers in a field feel a sufficiently thorough acquaintance with its species to undertake detailed analysis of variation within those species. The problem is restricted to those fields in which workers have accumulated large amounts of material from many parts of the ranges of the animals under investigation. Perhaps the most glaring omission in the fields represented was that of ichthyology. Its students are most cognizant of the problem, and lack of time, not of interest, prevented its inclusion on the symposium.

In addition to the biological significance of clines, it was felt important that inquiry be made into possible methods of handling the cline as a taxonomic entity. More than ten years have passed since Huxley pointed out the eventual necessity of some type of recognition, and it seemed appropriate to learn if any of the various fields has seen fit to adopt any of the various methods of designation of clines that have been suggested.

Participants

Introduction	•	James A. Peters Department of Biology Brown University
Mammalogy	•	William H. Burt Museum of Zoology University of Michigan
Ornithology	•	Charles G. Sibley Department of Conservation Cornell University
Herpetology	•	Charles M. Bogert Department of Amphibians and Reptiles American Museum of Natural History
Entomology	•	Theodore H. Hubbell Museum of Zoology University of Michigan
Malacology	•	William J. Clench Museum of Comparative Zoology Harvard University
Summary	•	J. Speed Rogers Museum of Zoology University of Michigan

The Subspecies Category in Mammals

WILLIAM HENRY BURT

IN THE early part of the present century collections of mammals were from widely scattered localities throughout North America, and nothing was known about the vast intervening areas. It was natural, therefore, to assign full specific rank to nearly every kind of mammal that was dignified with a latinized name. As collections increased, and as geographic gaps narrowed, it became apparent that some of the species had more or less unbroken ranges that extended to those of other named kinds. As a consequence, the number of species decreased and the number of subspecies increased.

At the time of Osgood's revision of the genus *Peromyscus* (1909) most of the named kinds of North American mammals were given full specific rank. Accordingly, there were some 28 species of *Peromyscus* that were destined to become subspecies or synonyms of what Osgood considered to be one species, *maniculatus*. Thus, it was Osgood's classical work that focused thinking in terms of the trinomial rather than the binomial, as had been common practice among his predecessors as well as many of his contemporaries. To cite two more examples, Miller listed 24 species of weasels (*Mustela*) in his 1911 checklist (1912) and 25 species in his 1923 checklist (1924); Hall (1951) reduced the number of species of weasels occurring over the same geographic area to three, with 60 subspecies. In the coyotes of the genus *Canis*, Miller (*op. cit.*) listed 14 species; these were recently grouped under one species by Jackson (1951), with 19 subspecies. This does not indicate that evolution has been going on in reverse. It does indicate that our interpretations now are quite different from those of students of 50 years ago.

Along with the change in evaluation of the lower categories, there grew up a school, of which I was one, of subspecies describers. I fear that the objective of many in this group was to discern small differences in samples of populations from different localities rather than to study the similarities of the samples, or the variability within a population. Our most horrible example of what can result from this indiscriminate naming of local populations is to be seen in the present literature on pocket gophers of the genus *Thomomys*. In one species, *T. bottae*, we now have listed more than 150 subspecies, and there are more to come. If this continues, eventually every colony of *Thomomys bottae* will bear a formal name recognized by the International Commission on Zoological Nomenclature. It is now necessary to have a large-scale map just to indicate the type localities of all the subspecies of *Thomomys bottae*. What does all this show from the biological point of view? It shows that *Thomomys bottae* is highly variable throughout its range. But is it necessary to have 150 or more names in the literature to show this? I think not. I sincerely believe that the variations in most of the morphological characters used as bases for naming the subspecies could be shown with symbols on a map, as some of the botanists have been doing with plants and as Blair (1953) attempted to do with *Peromyscus*. Blair's symbols

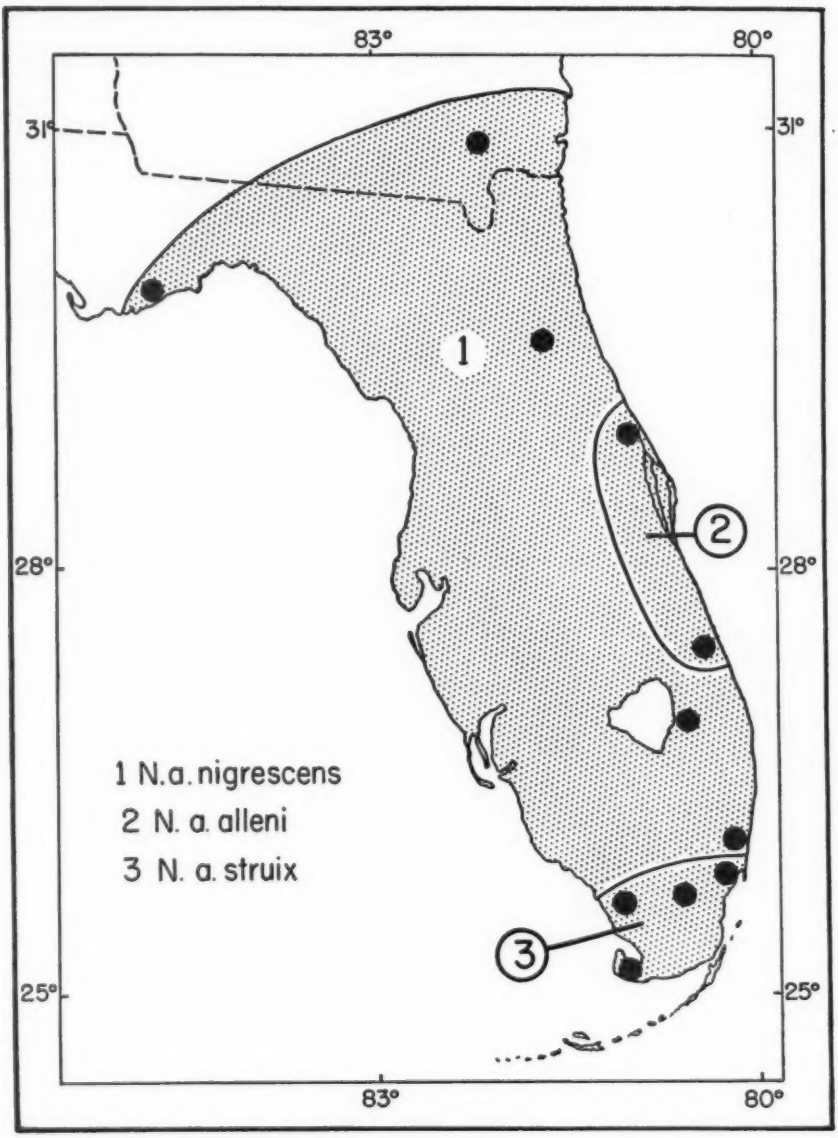

FIG. 1. Distribution of *Neofiber alleni* and its subspecies as interpreted by Hall and Cockrum. (After Hall and Cockrum, 1953.)

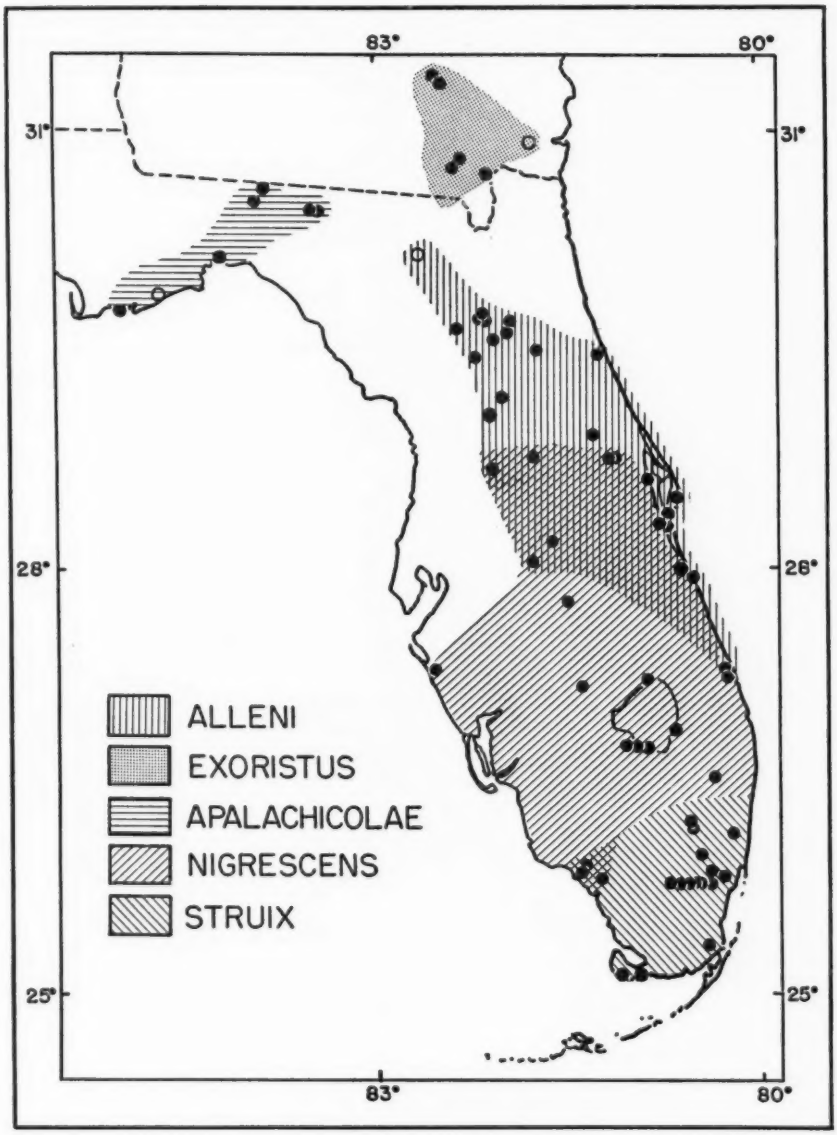

FIG. 2. Distribution of *Neofiber alleni* and its subspecies as interpreted by Schwartz. (After Schwartz, 1953.)

were too small and too crowded to give a clear picture, but the idea was good. Some of the ornithologists and entomologists have used the system of symbols with success.

A Case in Point

As an example of what can be done to give the reader a picture of the entire situation at a glance, I have selected a species of North American mammal, *Neofiber alleni,* that shows little variation throughout its range. This species was selected not only because of its lack of complexity in characteristics separating its subspecies, but because two papers, one a partial revision (Hall and Cockrum, 1953) and the other a revision (Schwartz, 1953), appeared in the same year with radically different interpretations of the same situation (Figs. 1, 2). The only reliable and usable character as yet detected to separate the subspecies of *Neofiber alleni* is color. But the true picture of this is obscured by the conventional system of mapping ranges for subspecies, as will be demonstrated later. In both papers just cited, the authors were patently influenced by previously described subspecies and their designated type localities, and, probably feeling obligated to preserve names, they built their arbitrary ranges around these artificially selected points. This is not biology in the strict sense.

If we look at the map by Hall and Cockrum (Fig. 1) we might be led to believe that the population at the extreme south of the range they outline for *nigrescens* is more like the population from the northwest panhandle area of Florida than it is like the population from the extreme south of Florida. This is not the case. Further, there is no biological or zoogeographical evidence of which I am aware that would warrant a range such as that given by them for *alleni.* Schwartz (Fig. 2) was more nearly correct in his interpretation, but again he fell into a trap when he tried to outline a range for *alleni,* the type locality of which happens to be in an area of intergradation, according to his interpretation of an intergrading area. Further, a series of specimens from 1.8 miles west of Flagler Beach, Flagler County, the northeastern limit of his range for *alleni,* are "dark, in fact darker than . . . any other specimen . . . of *alleni* and resemble the more southern *nigrescens* and *struix*" (Schwartz, 1953, p. 10). This kind of situation cannot be indicated on the conventional type of range map.

In Figure 3, I have attempted to indicate the degree of paleness or darkness by shading part or all of the circle. This is crude, to be sure, and is not based on numerical data. But it will indicate roughly the locations of the palest (open circles) and the darkest (solid circles) parts of the entire population of *Neofiber alleni* in its restricted range. With this method, local variants, such as the Flagler Beach population, are indicated. Further, it is quite evident that what Hall and Cockrum considered as *nigrescens* includes nearly the entire gamut of variation found in the species. The population from near Gainesville (*nigrescens* of Hall and Cockrum, *alleni* of Schwartz) shows up to be more similar to that from Georgia (=*exoristus* Schwartz) than it is to that from the type locality of *alleni* (Georgiana, Brevard County, Florida), and this is actually the case.

Conclusions

I believe that the two maps (Figs. 1, 2) demonstrate the arbitrary nature of the subspecies category as currently interpreted by students of mammals. I am of the opinion that *Neofiber alleni* and other continental species with more or less continuous ranges would be better understood if we were to discard the subspecific designations and concentrate on the variations and their behavior geographically. Some characters will be clinal in nature, others will not, but whatever the outcome, we should have a picture of the biological nature of the species.

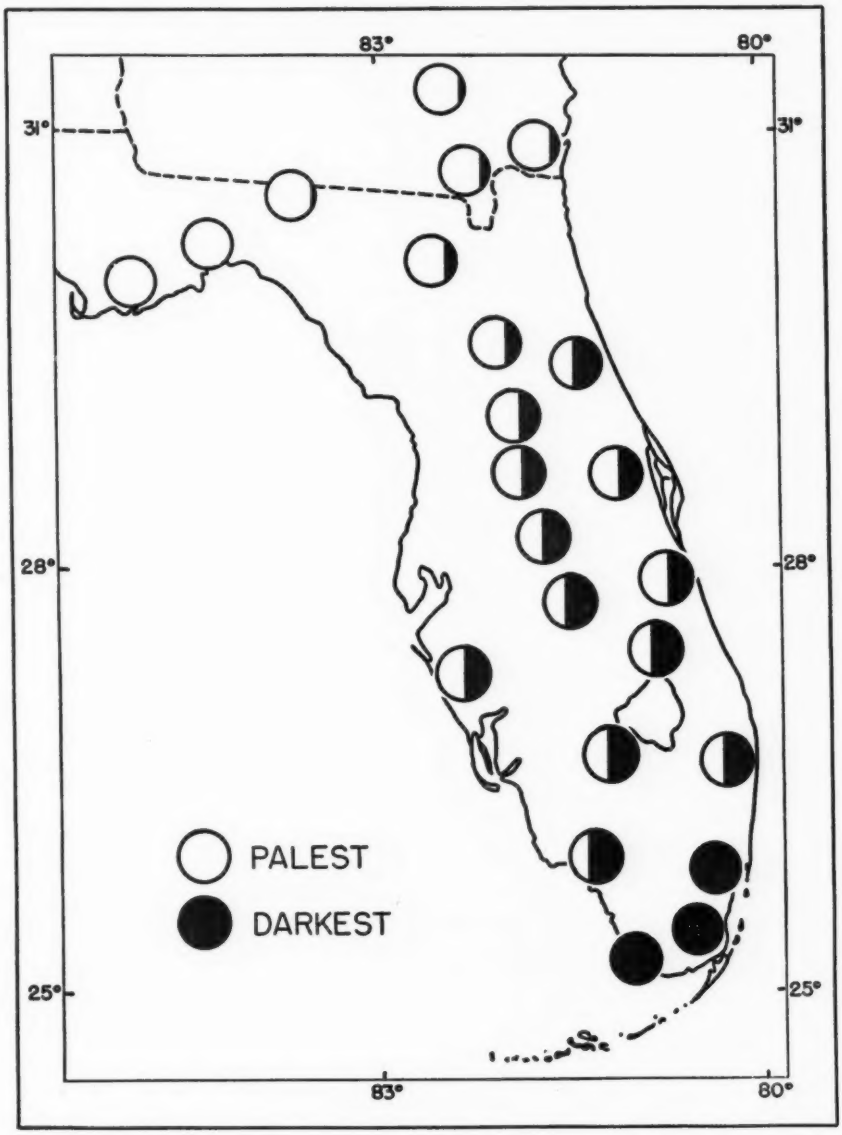

FIG. 3. Distribution of *Neofiber alleni* showing positions of palest (open circles) and darkest (solid circles) representatives of the entire population.

Isolated populations (on mountain tops or islands) present a somewhat different problem. Here, the judgement of the person working on the animals must be relied on. He should, I believe, base his decisions on the degree of morphological similarity or difference between the isolated population and the nearest continental one, unless he can take samples into the laboratory for breeding experiments. If, in his opinion, the isolated population warrants full specific rank, he should designate it as a species; if not, it should be treated with the similar, widespread population, without subspecific rank. I would avoid making hard and fast rules, because they always have their exceptions in biological matters. Many of our difficulties now stem from the fact that we have rules to which we try to adhere in every case. Rules are satisfactory as far as they apply, but we should not attempt to make them universally applicable for biology.

The rare case of two subspecies being separated and later coming together and behaving as species, as *Peromyscus maniculatus bairdi* and *P. m. gracilis* in Michigan, I believe could be taken care of with symbols and a short statement of the situation. I doubt if extra names help much, except to facilitate talking about them. But even then, it is necessary to mention the geographic area involved, so we have really gained little by using the trinomial.

Many authors, in this journal and elsewhere, have discussed the pros and cons of our present system. There is no need to repeat the arguments here. My only purpose is to present a case in mammalogy and suggest a possible substitute for our present system.

REFERENCES

Blair, W. F. 1953. Factors affecting gene exchange between populations in the *Peromyscus maniculatus* group. *Texas J. Sci.*, No. 1: 17–33.

Hall, E. R. 1951. American weasels. *Univ. Kan. Publ., Mus. Nat. Hist.*, *4*:1–466.

Hall, E. R., and Cockrum, E. L. 1953. A synopsis of the North American microtine rodents. *Univ. Kan. Publ., Mus. Nat. Hist.*, *5*: 373–498.

Jackson, H. H. T. 1951. Classification of the races of the Coyote. The clever Coyote, Pt. II. Harrisburg, Pa., The Stackpole Co., and Washington, D. C., Wildlife Mgt. Inst., pp. 227–341.

Miller, G. S., Jr. 1912. List of North American land mammals in the United States National Museum, 1911. *U. S. Nat. Mus. Bull.*, 79, xiv + 455 pp.

——— 1924. List of North American Recent mammals, 1923. *U. S. Nat. Mus. Bull.*, 128, xiv + 673 pp.

Osgood, W. H. 1909. Revision of the mice of the American genus Peromyscus. *N. Amer. Fauna*, No. 28, 285 pp.

Schwartz, A. 1953. A systematic study of the water rat (*Neofiber alleni*). *Occ. Pap. Mus. Zool. Univ. Mich.*, No. 547, 27 pp.

The Contribution of Avian Taxonomy

CHARLES G. SIBLEY

IT IS appropriate that the views of ornithologists should be represented in this symposium because it was an ornithologist who first used trinomials to designate geographic races; it was primarily the ornithologists in this country who first espoused the concept, and it has been, I regret to say, in considerable measure due to the efforts of a few ornithologists that the subspecies has fallen into disrepute.

It was Hermann Schlegel, as the coauthor with C. J. Temminck of the Aves section of Siebold's *Fauna Japonica* published in 1844, who first applied a trinomial combination to designate geographic subdivisions of species. There were few proponents of this system in Europe at first, but Baird, Coues, and Ridgway in the United States adopted it and applied the triple combination to geographic races. Coues even went to England in 1884 and in an historical meeting at the British Museum he tried to persuade the leading British avian taxonomists of the time to adopt the trinomial system. He was supported by Henry Seebohm but rebuffed by such potent adversaries as P. L. Sclater and R. Bowdler Sharpe. One result of this defeat was the adoption of the Code of Nomenclature of the American Ornithologists' Union in 1885. The watchword of the time was, "Intergradation is the touchstone of trinominalism." By 1912, following the deaths of Sharpe and Sclater and the increasing influence of Ernst Hartert, the subspecies became as entrenched in Europe as it was in this country.

It may be that history is not our purpose here but it seems apparent that the transition from the strict application of binomials to that of trinomials contains many parallels to the present situation. The problems which confronted our predecessors in systematic zoology are remarkably similar in kind, although different in degree, to those which face us today. Before attacking the subspecies concept too vigorously let us examine history once more for evidence as to its causes, its effects, and its values.

In the century between Linnaeus and Darwin species were regarded as comfortably immutable and collections were still too limited to demonstrate the true range of individual and geographic variation. By 1859, when Darwin provided the theoretical basis to explain such variability, collections were extensive enough to reveal it, and Schlegel and others had indicated a method for its nomenclatorial recognition, namely, the trinomial. A modification in nomenclatorial practice was inevitable if Darwinism was to be applied. As late as 1909 Sharpe retained the Linnaean binomial in his *Handlist* and thereby emerged with a count of over 19,000 "species" of birds in the world. The enormous difference between this figure and the 8,600 computed by Mayr and Amadon in 1951 is an index to the differences in viewpoint of the authors and their times.

We are today in a position curiously parallel to that of systematists during the transition from binomialism to trinomialism. Let us approach the present problem with an understanding of the historical background as well as of its biological significance, for it is probable that Coues and

Seebohm felt that they were as "modern" and "progressive" as do those today who call for the death sentence to be handed down against the trinomial.

We have arrived at this point by the same inevitable route which was travelled by our predecessors. Collections have continued to grow, ideas have continued to expand. When the subspecies concept was coming into widespread use there was no science of genetics to provide explanations of the mechanics of variation, and the use of statistical analysis based upon large series from many localities was an impossibility. The early systematists did the best they could with the materials at hand and that is what we will continue to do, whether we like it or not, for in this we have no choice.

Current Opinion

It is apparent, then, that continued refinement of concepts and analytical techniques has brought systematic zoology to the point where many workers are dissatisfied with current practices employed in the nomenclatorial treatment of infraspecific categories. The purpose of the present paper is to report on the current practices in avian systematics and the suggestions for improvements which have been proposed by ornithologists.

Avian subspecies are still being described. Some of them certainly are not worthy of nomenclatorial recognition but extreme "splitters" are not peculiar to avian systematics alone. On the other hand, there is, on the part of the majority of avian taxonomists, a healthy feeling of antagonism toward sloppy taxonomic work. Dissatisfaction with the trinomial is far from new in ornithology.

There were many anti-subspecies whispers before 1939 when Huxley gave us a coherent account and added the word "cline" to our vocabulary. In 1942 he reviewed many instances of clinal variation (1942, pp. 174–227) and proposed the term "micro-subspecies" for small or weakly differentiated populations which were not to be named since to do so would unnecessarily complicate the nomenclature Huxley rejected the terms "micro-race" proposed by Dobzhansky (1937) and "subsubspecies" proposed by Goldschmidt (1940).

Huxley (1942, pp. 225–226) proposed a scale of values with "0" at one end and "100" at the other to designate clinal variation. Populations of equal value on such a scale could be connected by a line termed an "isophene" or a "pheno-contour." He further proposed (1942, p. 253) the term "genocline" for the gradient produced by hybridization and subsequent back-crossing, in other words, introgressive hybridization. The analysis of Huxley's "genocline" was first accomplished by botanical workers (Anderson, 1949) and one method, that of the crude but useful "hybrid index," has been employed by the present author in the analysis of avian hybridization (Sibley, 1950).

Huxley urged (1942, p. 406) that "subspecies should connote a moderate degree of difference, not mere difference, however minute." He suggested further that no new nomenclatorial category be introduced but that descriptive statements or designation by letter or number be employed.

In 1941 A. H. Miller in reference to *Junco oreganus* noted: "Over a wide area it is doubtful if true racial units exist; instead there are many independent geographic gradients in characters that run in different directions through the area. One can recognize some poorly defined breaks in the gradients that permit the mapping out of races that combine certain average values for various characters, but these races are in a sense artificial."

Mackworth-Praed (1943) in commenting upon the disparity of viewpoints represented by Huxley's clinal concept and Clancey's naming of local populations of Scottish birds recommended that minutely distinguished "races" should be pointed out but not named. He further noted that if such "subraces" were to be dealt with nomenclatorially we would need to use

four or five (or more) names to express equality in terms of differentiation. This could result in tagging the wren of Scotland with a combination like *Troglodytes troglodytes troglodytes troglodytes indigenus.*

Harrison (1945) suggested a "bifid racial terminal" to indicate the character of intermediate populations in terms of described subspecies. Thus, for example, a population of the European jay might be characterized as

Garrulus glandarius < *G. g. rufitergum* / *G. g. glandarius*

for a population intermediate between but most like the race *rufitergum,* and

Garrulus glandarius < *G. g. glandarius* / *G. g. rufitergum*

for a segment of a cline intermediate but more like *glandarius.*

Lack (1946) questioned whether trinomial terminology had not outlived its usefulness and validity, and Tucker (1946) suggested that it may be a truer representation of facts to say that a subspecies shows a tendency to be browner in one locality and grayer in another rather than to subdivide further. These remarks of Tucker's were made at a meeting of the British Ornithologists' Club in reference to a paper presented by Clancey (1946) advocating the recognition by formal trinomial of every distinguishable population of British birds, regardless of the degree of difference involved. Southern (1946) also commented on Clancey's paper, expressed opposition to his viewpoint, and called attention to the statistical weakness of Clancey's arguments.

Moreau (1948) indicates his belief that the naming of subspecies which are segments of a cline can be justified only if discontinuities in the gradient can be defined and located.

In discussing geographical variation in the European Robin, Lack (1951) concludes: "While subspecific names have been retained . . . it is arguable whether they are not . . . more misleading than helpful in describing this complex situation—a situation which may well be found not unusual in birds when more is known. . . . In the Robin, at least, the use of trinomials gives not merely an inadequate but a misleading picture of the natural variation, and it is both simpler and more precise to describe the trends of variation in terms of geographical areas, omitting subspecific names altogether."

Bullough (1945) in commenting on the nomenclatorial recognition of physiological races suggests that we might follow Huxley (1940, p. 28) and add the designation "(phys.)" to indicate such a race. This suggestion was quickly rebuffed by Wagstaffe and Hincks (1945) who urged that physiological races should be designated by some non-nomenclatorial system to avoid the complications which would be certain to follow in regard to synonyms and other problems.

The opinions of Wilson and Brown (1953) have recently appeared in this journal. They have taken certain ornithologists to task, and justly so, for adherence to the trinomial when the material under study might better have been attacked from the clinal viewpoint. They have suggested, as have others, that a statement of locality or range is preferable to a formal latinized trinomial.

In response to my invitation to comment upon the question of "the subspecies versus the cline" Ernst Mayr replied (letter, November 16, 1953) that it was his opinion that:

> . . . subspecies and clines are concepts belonging to different fields. A population can belong to only one subspecies but it can belong to several different clines. In other words, the subspecies is a taxonomic concept while a cline is an evolutionary one. Nothing is gained by naming clines. They can be referred to descriptively but that is all. For instance, among Australian birds there are almost invariably at least two clines involved: one south-north cline of decreasing size toward the Equator, and a second cline from the periphery of Australia toward the interior of decreasing pigmentation. I do not think subspecies versus clines is a legitimate alterna-

tive. You cannot base a classification on completely overlapping criteria.

The real alternative is, subspecies or no subspecies. We must realize that we have reached a point where nearly everyone is getting fed up with excessive splitting.

The real question is what an author wants to achieve in a given paper. If he merely wants to study variation and trends of variation, he might as well omit all reference to subspecies. However, if one wants to emphasize degrees of distinctness of geographical isolates, one can do so much better by employing subspecific names. To designate populations merely by locality names does not bring out the fact that some are slightly different and others drastically so. With locality names we can designate only fixed spots on the map. With subspecies names we can designate phenotypically similar populations regardless of geography. Since it is the object of the classifier to designate such phenotypically similar populations, I don't see how, particularly in insular regions, he can do without subspecies, but he must realize at all times that the subspecies is a strictly arbitrary taxonomic concept.

Frank Pitelka replied in a letter dated December 2, 1953:

. . . my work on two genera of birds, unrelated and presenting rather dissimilar problems when considered in detail, has led me to realize that the basic facts of character geography and ecological correlations are seriously obscured when forced into the framework of presentation on the subspecies basis that is standard for modern taxonomic revisions. The quantity of detail, the preciseness of the questions motivating the research, and the level of analysis are now such that the subspecies as a basic unit no longer facilitates but hinders straightforward presentation and exploration of facts. I am not prepared to say that we should completely eliminate the subspecies as a taxonomic unit and it may be true that those who wish to refer to intraspecific population units merely by geographic terms may be awkward about it. Between the former and the latter there may be some happy compromise. What I am maintaining now is that the old way is farther to one side of that compromise than the new way; therefore, that the standard approach is at least less successful than the one proposed by Lack, the Harvard entomologists, and others.

Discussion

It is apparent from the foregoing citations and statements that ornithologists have been concerned for some time with the problem of the taxonomic treatment of clines. The inadequacy of the trinomial as a means for the description of clines is obvious but the proposals for modifications using names offer but slight improvement. It will avail us little to increase the number of names because the problem deals with a continuum and the only practical means for describing such phenomena is a numerical one.

One point of confusion involves the feeling that we must deal with clines and subspecies as mutually exclusive concepts rather than as different methods, each applicable to particular situations. Mayr's statement that "a population can belong to only one subspecies but . . . to several different clines" sums up a viewpoint which needs to be emphasized. Another point is that made by Moreau (1948) who believes that the naming of clinal segments is justified only when discontinuities in the gradient can be defined and located.

These ideas may be summarized graphically by Figure 1. The theoretical situation portrayed is of common occurrence in birds. Discordant clines involving color and size are interrupted by barriers to the distribution of the species involved. Gene flow within each population (*A*, *B*, *C*) is

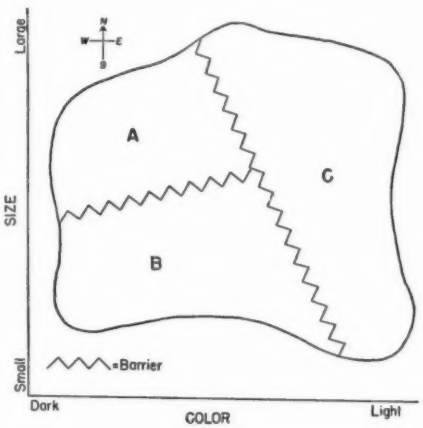

FIG. 1.

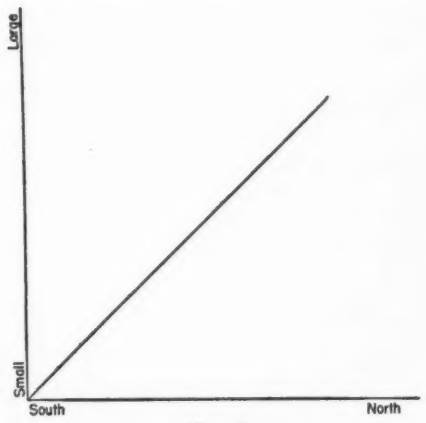

FIG. 2.

uninterrupted. The result is that the theoretical clinal trends of color and size are somewhat flattened owing to free gene exchange within each population and that a relatively sharp "step" occurs at the barriers. Thus, if the barrier were not present between *A* and *B* the size cline theoretically would be as in Figure 2. The presence of the barrier modifies this cline so it actually appears as in Figure 3.

A justifiable taxonomic procedure in this case might be to name as subspecies the populations designated as *A*, *B*, and *C*. It would not be justifiable to split *C* on the basis of north-south size differences because no discontinuities could be demonstrated. The fact that the size and color clines are discordant does not of itself invalidate the naming of subspecies. What is important in this regard is that the boundaries of the subspecies shall coincide with clinal discontinuities. This in essence means coincidence with barriers of sufficient effectiveness to interrupt gene flow and permit the isolation which is the *sine qua non* of differentiation.

Referring again to Figure 1 it is obvious that there could be other clines running in discordance with both color and size. It is also apparent that in nature not all clines "step" conveniently at the same places. Critics of the thesis that clines and subspecies can co-exist will be quick to point these problems out. The solution will vary with the individual situation; in a general discussion only working principles can be defined.

A frequently noted criticism of the validity of a subspecies is that it is a "color race," a "size race," or a "physiological race," meaning that it is based primarily (or entirely) upon a discontinuity in only one character. Should this invalidate the application of a trinomial? Again generalities will not suffice. Individual situations will have to be judged on their own merits. However, if a sharp break or step is present in the color cline, for example, it must be there because of an interruption in gene flow or a sharp environmental change. If either is true then other characters also will probably show discontinuities. Before condemning a race seemingly based on a single character other possible discontinuities should be sought. There are many examples of names once synonymized which have been restored to use and the original author proved "right for the wrong reasons."

If we grant that the trinomial has been abused and that it will not describe clinal variation satisfactorily, but that for insular populations or those with coincident discontinuities at their borders it serves a useful function, we are left with the necessity of developing more satisfactory meth-

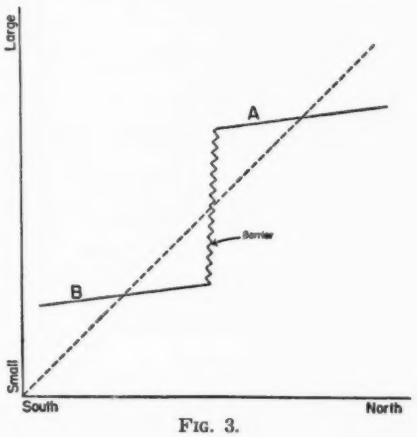

FIG. 3.

ods for the description of clines. Certainly the methods involving name multiplication must be rejected. If the trinomial has been overworked think of what would happen if we gave the extreme splitters a quadrinomial to toy with! The "bifid racial terminal" of Harrison (1945) or similar systems do not go far enough in describing degrees of intermediacy. Utilizing simply locality designations coupled with character descriptions may be satisfactory for problems dealing with few localities and a limited number of characters but could become burdensome for writer and reader alike when many localities and characters are involved.

If all the clines in a situation are concordant the description is greatly simplified. It is probable that complete clinal concordance will exist only when the clines are the result of introgressive hybridization. This is because such clines depend upon gene exchange between the hybridizing parental populations rather than the effects of local selection as in "normal" clines. Hybridization on a scale which permits the establishment of hybrid clines is rare in birds but in the genus *Pipilo* in Mexico (Sibley, 1950 and ms.) hybrid gradients have been described quantitatively using a numerical "hybrid index" for color analysis which is found to be concordant with the size cline as determined by weight. Devising more elaborate numerical methods for describing two or more discordant clines will depend upon the inventiveness of future workers and what they are trying to describe. It is this writer's belief that problems of this sort are self-solving. Faced with the need for devising a method of description which fits the pattern in nature, taxonomists will be forced to design new techniques. Let us avoid additional formal "rules" of nomenclature in this case and recognize that we are dealing with problems which approach infinity in the variety of their themes.

Summary and Conclusions

1. The present dissatisfaction with the trinomial is due to its inadequacy in describing the infraspecific variation revealed by growing collections and changing concepts.

2. Clinal variation is especially difficult to express in terms of the trinomial.

3. Various methods have been proposed to adapt nomenclature to the clinal concept. Most suggestions propose that a system be devised which does not involve formal nomenclatural recognition of clines.

4. No completely acceptable method of expressing clinal variation has as yet been devised.

5. It is not necessary to eliminate the trinomial from usage in order to develop clinal terminology. The description of clines is an addition to the present system, not a substitute or a replacement.

6. Numerical systems may offer the best solution to clinal description.

I am indebted to Alden H. Miller and Josselyn Van Tyne for their kindness in reading the manuscript. Both have expressed general agreement with the opinions and suggestions presented.

REFERENCES

ANDERSON, E. 1949. Introgressive hybridization. John Wiley & Sons, New York.

BULLOUGH, W. S. 1945. Physiological races and nomenclature. *Ibis, 87*:44–48.

CLANCEY, P. A. 1946. A review of some recent researches, with remarks on the possible outcome of the present intensive racial survey of British birds. *Bull. Brit. Orn. Club, 66*:86–90.

DARWIN, C. 1859. On the origin of species by means of natural selection, ... John Murray, London.

DOBZHANSKY, TH. 1937. Genetics and the origin of species (first ed.). Columbia Univ. Press.

GOLDSCHMIDT, R. 1940. The material basis of evolution. Yale Univ. Press.

HARRISON, J. M. 1945. Races, intermediates and nomenclature—a suggested modification of the trinomial system. *Ibis, 87*:48–51.

HUXLEY, J. S. 1939. Clines: an auxiliary method in taxonomy. *Bijdr. tot de Dierkunde, 27*:491–520.

——— (editor). 1940. The new systematics. Oxford Univ. Press.

——— 1942. Evolution: the modern synthesis. Harper and Brothers, New York.

(Concluded on p. 125)

The Indication of Infraspecific Variation

CHARLES M. BOGERT

IN DEALING with the phenomena of variation, it is of little importance whether infraspecific populations are given nomenclatorial recognition; but it is of considerable value to ascertain the nature and the extent of the variation within any species. Among reptiles and amphibians ontogenetic changes as well as sexual dimorphism often complicate the procedure. It is necessary first to ascertain the extent of variation within local populations. Once this information is available local populations can be compared, and virtually always it is possible to demonstrate geographical trends in variation.

There are several methods that can be used to indicate the complexity of the variations encountered in any species. The method selected will depend upon the nature of the variations observed as well as upon the size of the samples. Symbols can be plotted on maps for individual characters, or population formulas can be devised. For some sorts of data the Dice-Leraas method provides an adequate means of demonstrating the nature of the trends observed, or even simple bar diagrams can be employed. When data have been obtained for a sufficient number of characters it is virtually always possible to demonstrate the existence of divers geographical trends, continuous in some characters, discontinuous in others. Or there may be reversals or abrupt changes in trends, usually accompanied by discontinuities in distribution or in ecological factors.

After several characters have been plotted, or at first merely tabulated in geographical sequence, it is often possible to delineate areas inhabited by populations that share more than one characteristic not possessed by populations in other parts of the range inhabited by the species as a whole. When the differences are of sufficient magnitude there are advantages in nomenclatorial recognition of such distinctive populations.

The mere pigeonholing of populations at infraspecific levels, especially when the range of variation has not been ascertained for several characters, conveys a false impression of uniformity, as Huxley pointed out in 1939. However, the belief that clines within species preclude the possibility of recognizing subspecies is based upon an equally false assumption. For if names are not employed to designate recognizably different assemblages of individuals within the species, an equally false impression of uniformity is conveyed by the use of the specific name alone. As Moore has shown in his study of the common North American frog, *Rana pipiens*, when clines are involved they may affect breeding potentialities as well as phenotypic characters; individuals drawn from populations at opposite ends of a cline may be as different reproductively as they are phenotypically. If there is no conspicuous discontinuity in more than one character, it may, of course, still be unprofitable to designate populations within the cline.

On the other hand, subspecies can be recognized when sharp discontinuities can be demonstrated. After several characters of a species are tabulated, assuming that sufficiently large samples are drawn from

various parts of the range, it can often be demonstrated that discontinuities are correlated with disjunct distributions or with abrupt changes in the environment. Exceptional species are more tolerant (probably more readily adaptable) to varied environments, and their ranges may be virtually continuous. In such cases no conspicuous discontinuities in character trends may be discernible. Under these circumstances the definition of subspecies or their distributions is so arbitrary as to be meaningless either taxonomically or biologically. Little is gained by the application of names to portions of a continuous cline.

To summarize, it is within the province of the taxonomist to describe the clines usually encountered in several characters of any one species. Subspecies should be recognized only when sharp discontinuities in the trends of one or more individual characters can be demonstrated. Their recognition should not be attempted until careful analysis has been made of the trends in several characters. Contrary to the belief of those who have never bothered to analyze more than a few characters, it can often be shown that discontinuities in several characters occur in the same, or in approximately the same, area. Since clines reflect the adaptive responses of local populations to their environment, this condition is most likely to be encountered where there are abrupt changes in the environment. However, the situation may also result from disjunct distributions, where there is no gene flow between isolated populations of a single species.

Taxonomists who ignore infraspecific variation and devote their efforts to naming and describing species, or at worst only specimens, shun the ecological and evolutionary implications of taxonomy, which in the words of Julian Huxley should be that of "detecting evolution at work."

REFERENCES

HUXLEY, J. S. 1939. Clines: an auxiliary method in taxonomy. *Bijdr. Dierk.*, *27*:491–520.

MOORE, J. A. 1944. Geographic variation in *Rana pipiens* Schreber of eastern North America. *Bull. Amer. Mus. Nat. Hist.*, *82*: 349–369.

The Naming of Geographically Variant Populations

or *WHAT IS ALL THE SHOOTING ABOUT?*

THEODORE H. HUBBELL

ENTOMOLOGICAL taxonomy at the subspecific level is in a chaotic state as compared with the situation in most vertebrate groups. There is little agreement, either as to the categories of infraspecific variation that ought to be recognized (Sabrosky, 1940), or as to which and how many of them should be named. The reasons for this state of affairs are to be found in (1) entomologists, (2) insects, (3) ignorance, and (4) nomenclature.

Entomologists, or to be more precise, entomological taxonomists, probably far outnumber all other taxonomists combined. Among them are to be found many highly trained biologists and perhaps an equal number of competent self-taught amateurs, some of whom are leading authorities in their special fields. The systematic work of such students commands attention and respect; some of it has theoretic importance, and all of it is done in the light of the implications of modern evolutionary theory. Then there is the great group of workaday taxonomists whose main job, as they see it, is to get on with the description and naming of the estimated one to several million species of insects still undescribed. For the most part these men are seeking morphological "characters" by means of which to discriminate between or to group similar species. These "species describers" commonly work with small numbers of specimens from few localities, and thus it is seldom that they must deal with clinal or other geographic variation. Theirs is an essential task, and they do it on the whole well and conscientiously; but for all the evidence their work shows of the influence of the "new systematics" it could as well be pre- as post-Darwinian. Finally we have the dilettante collectors and opinionated tyros, who can and sometimes do publish taxonomic papers. Some delight in multiplying names, giving to every variant specimen a tri- or polynomial Latin tag as variety, subspecies, race, aberration, form, transition form, or [presumptive] hybrid—to list only the most often used pigeonholes. Obviously it is not likely that entomologists, so diverse in background, viewpoint, and objectives, will ever fully agree on how to treat subspecific entities.

Insects are the biggest and most varied group of animals, and this fact has important consequences and implications for taxonomists. The variety of insects in every aspect of their existence is almost beyond belief. Think of the enormous range in form, size, vagility, longevity, reproductive potential, type of life history, food habits, and all the other varied aspects of ecology; is it any wonder that a specialist in one group often is inclined to reject the subspecific treatments adopted in some other group, simply because he has seen nothing comparable among the insects he knows best? Geographic differentiation in species of the gall-wasp genus *Cynips* is not much like that encountered in grasshoppers of the genus *Melanoplus;* the former is conditioned by the host-parasite relationship, while grasshoppers have a more generalized relation to their envi-

ronment, more like that of the small mammals, which they resemble in their mode of geographic differentiation. There appears to be far more diversity among insects than among vertebrates in the factors that may produce isolates within species, and the entomologist may consequently have to deal with a greater variety of resultant taxonomic situations.

Another consequence of the immense size of the class Insecta is our almost complete ignorance concerning the vast majority of its species. If we take Sabrosky's 1952 estimates as our basis, about two-thirds of a million insect "species" have been described, and the total number in existence is probably several million. Of those species already described, all that we know about most is a few morphological details and the fact that they have been taken at one or a few localities. The majority are represented in collections by single specimens or small series. This state of affairs will certainly persist indefinitely, for no matter how fast entomological knowledge increases, the species describers are bound to keep far in advance of it. In this situation we find a prolific source of nominal "subspecies" that are set up almost by accident. "Species" are described from different localities on the basis of small series that differ in morphological characters. Later discoveries tend to bridge the gaps, and the "species" are reduced to "subspecies" under the oldest name. Our lists are filled with arrays of such nominal "subspecies," formed unintentionally, the actual status of which is unknown. They exist in limbo, and only revision on the basis of adequate collections can either eliminate them as synonyms or give them real meaning. Such a revision may not be forthcoming for years or for generations.

Not all the biologist's woes stem from the cussedness of nature; some he creates for himself. Among the latter is the Linnaean system of nomenclature when he tries to apply it to situations for which it was not devised and to which it is not suited. This system, which assumes the separateness of the things it categorizes, still works well down to and including the species of a given time-level. This is because species *are* discrete entities, both in museum practice and by the criteria of modern evolutionary theory. But when we deal with entities that lack definite limits and grade into one another, as do most infraspecific segregates, then name-systems of the Linnaean type do not and, in my opinion, cannot be expected to meet the needs of the situation.

It may be paradoxical, but the fact remains that it is to those species we know best that we are least able to apply orthodox taxonomic concepts and nomenclature. Even when the trinomial is grafted on to the Linnaean system we find ourselves unable to deal satisfactorily with one of the commonest and simplest of subspecific taxonomic situations, the clinal variation of a character within a population. Unlike the species boundary, which we may define as effective reproductive isolation or as a morphological difference which we assume involves such isolation, there is no agreed-upon criterion for subdividing a clinally varying population. Subspecific names can be applied only by making arbitrary decisions as to how many and which segments of the population shall be named. Such decisions are likely to be strongly influenced by the number of names available and the position of their type localities. Thus, among the grasshopper species of the eastern United States which show north-south clinal variation, some have escaped subdivision, and some are divided into two "races" or subspecies separated by "broad regions of intergradation." By contrast, the little grouse-locust *Nomotettix cristatus* (Scudder), which shows clinal variation in pronotal cristation and which had eight available names, was cut into five subspecies by Rehn and Hebard (1916), into four by Blatchley (1920), and into a slightly different five by Hebard (1934).

If we deal with more than a single taxonomic character, the clinal variations in each of them rarely coincide, even when

the species has a linear type of range. The various combinations are generally too numerous and too varied and at too many levels of differentiation to fit any predetermined set of categories, and no two situations are alike. When we try to present the results of our study of one of these situations, it usually turns out that we have no trouble in describing it so that others can understand what we have found. All the difficulty and argument centers about the *nomenclature*—what names should be used, and which of the population segregates should be named. But this is a semantic, not a biological problem. No matter how we place the labels, they add nothing to our understanding of the situation. Often, in fact, they may obscure it by covering up with a stereotype some peculiarity that would invite closer scrutiny if it had been simply described and not named.

After much reading, argument, and discussion on the taxonomic aspects of infraspecific variation, and a certain amount of solitary thinking, I have reached conclusions that are satisfying to me. Essentially they amount to the belief that population analysis below the species level is too complex to be bound by formal taxonomic and nomenclatorial rules, and that each case must be considered on its own merits and treated by whatever method seems best suited to it. This idea is not original; in fact it is becoming rather general, though not, I fear, among entomologists. I speak from that company, not for it. This approach does seem to make my own studies more meaningful, permits any desired degree of flexibility in presentation of results, and is based on the premise that classification is and will remain as much an art as a science. The taxonomist requires rules; but the new systematics has opened a whole new field of studies in which the old rules of nomenclature are neither helpful nor relevant. In the examples which follow will be found illustrations of the generalities discussed above, taken from the Orthoptera, the group I know best. After presenting them I shall summarize the ideas to which consideration of such cases has led me.

Subspecies and Clines in Orthoptera

The taxonomy of the Orthoptera is probably as advanced as that of any order of insects. In this country we have had a number of exceptionally able students of the group, among whom the unquestioned leader has been James A. G. Rehn of the Academy of Natural Sciences of Philadelphia. Perhaps owing in part to Rehn's early training in mammalogy, the concept of the subspecies as being equivalent to the geographic race has for many years been standard among workers in Orthoptera. We have long since ceased to be bothered by the naming of color variants, aberrations, seasonal forms, and the like. Fulton's demonstration of the existence of "ecological races" in crickets of the genera *Oecanthus* (1925, 1926), *Nemobius* (1931), and *Acheta* (1952) has been almost the only discordance, and would have been a source of difficulty to those who seek complete consistency in taxonomic treatment within a group were it not that Fulton has generally avoided the pitfalls of a technical nomenclature. In his latest paper, on *Acheta,* he says that there are in North Carolina "at least four populations of field crickets which may be so reproductively isolated from each other as to constitute biological, physiological, or ecological species, subspecies, or races, whichever you prefer to call them." They may well be "sibling species," at least in the instances of *Nemobius fasciatus* and *Acheta assimilis;* but here are excellent examples of the uselessness of such theoretical distinctions in practice. Fulton calls the four "races" or "sibling species" of *Acheta assimilis* found in North Carolina *Triller, Woods, Mountain,* and *Beach.* They can be told apart in life, but museum specimens are morphologically indistinguishable because of the wide range of variation in each "race." Latin names might have been dug up for them from the voluminous synonymy of *Acheta assimilis,* but what

would have been gained? The name *Acheta assimilis* covers them all; most specimens cannot be more closely named. Only when specimens are accompanied by data on song and habitat can they be assigned to one or another of Fulton's "races," and his well-chosen colloquial names seem likely to serve all purposes of description and discussion for that small group of workers who will be concerned with this situation.

The following examples of geographic differentiation in Orthoptera are not exhaustive, but merely illustrative of different levels of complexity and different modes of taxonomic treatment.

Example 1. *Mermiria maculipennis* Bruner (Rehn, 1919, pp. 102–117). This slant-faced macropterous grasshopper, an inhabitant of dry grassland, ranges from southern British Columbia, North Dakota, and southern Wisconsin, south to the Gulf coast of Texas, northern Durango,[1] and southern Arizona and Nevada. It shows a striking north-south clinal change in morphological characters and coloration, complicated by local variations in size and robustness. In the north it is relatively small, dark, and stubby, with a pronotum that is angulate behind and not constricted in the middle, relatively long antennae, and large eyes in the female. Southward it becomes larger, generally paler, and more elongate, and has a pronotum that is decidedly saddle-shaped and less angulate behind, proportionately shorter antennae, and smaller eyes in the female. Differences between the extremes are marked, and northern material was confused with another species, *M. bivittata,* until McClung in 1917 showed that *"bivittata"* was divisible into two groups on the basis of a difference in the form of one chromosome in the male germ cells. Rehn described the northern part of the *maculipennis* population as the subspecies *macclungi;* the southern part was treated as *m. maculipennis,* and the populations of the broad intervening zone he divided into belts of atypical *macclungi,* intermediates, and atypical *maculipennis.* In 1931 Hebard placed as atypical *macclungi* most of what Rehn in 1919 had called intermediates. In this species the changes in coloration, pronotal form, elongation of body, and head proportions are rather closely correlated, so that it is quite feasible to name the extremes as geographic subspecies, even though their limits must be subjectively determined.

Example 2. *Ceuthophilus uhleri* Scudder (Hubbell, 1936, pp. 301–315). This wingless camel-cricket is a species of the eastern deciduous forest region, ranging from Iowa and Kansas east to southern New York and coastal Virginia, and south in a narrowing wedge to the Gulf Coast in Alabama and Florida. It shows a centripetal pattern of clinal variation in two characters of the genitalia (Fig. 1), one of the sternum, and one affecting the proportions of the legs and their spinous armature. Populations inhabiting Indiana, Maryland, and Florida are more similar in respect to these features than any of them is to the central population in northern Alabama. The isovariant lines or isophenes form contours centering on northern Alabama and running out along the Appalachian axis. Superimposed on this cline of covariant characters is another, a north to south increase in size, which tends to obscure the resemblances of the peripheral populations. Without attempting to analyze the possible causes of such a distribution, Hubbell treated *uhleri* as a single species without subspecies, but with the different parts of the population designated by symbols for the purpose of discussion, and with their characteristics graphed. An attempt to apply conventional nomenclature to this situation would have resulted in a peripheral subspecies extending from Florida to Iowa to New York in a ring around a central subspecies, which seems absurd.

Example 3. *Aptenopedes sphenarioides* Scudder (Hebard, 1936, pp. 210–218). This is a subapterous spine-breasted grass-

[1] Specimens in the University of Michigan Museum of Zoology.

hopper that occupies a limited range comprising most of Florida and adjoining parts of Georgia and Alabama. It inhabits a region which has been flooded and drained by the sea several times during the Pleistocene (see Olson, Hubbell, and Howden, 1954); the species population has undoubtedly been fragmented and reunited more than once. Local populations differ considerably in size and coloration, but not in any regularly clinal way. The principal morphological difference evident upon superficial inspection is in the shape of the male cercus; this structure is simply awl-shaped in the north, and becomes curved and apically falcate in the south. In 1902 Rehn described southern material as a distinct species, *clara;* later this was reduced to a subspecies of *sphenarioides.* It was long supposed that the situation was simply that of two subspecies connected by a broad zone of inter-

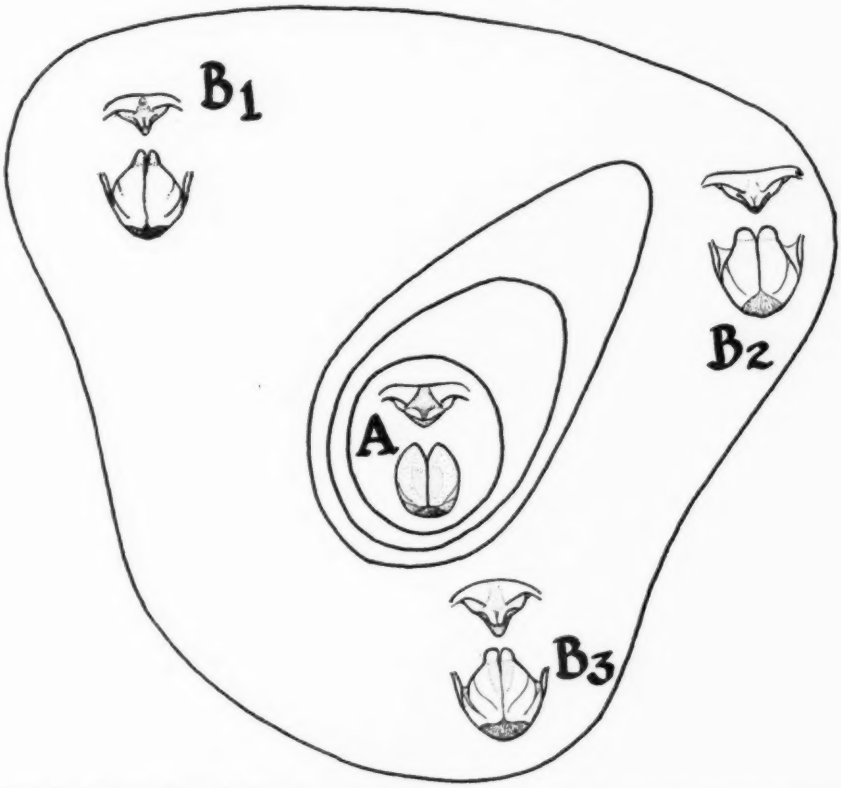

FIG. 1. The centripetal cline in male genital characters of *Ceuthophilus uhleri* Scudder, semi-diagrammatically shown. Population *A*, in north-central Alabama, has the apices of the epiproct (upper figure) and subgenital plate (lower figure) unconstricted and the marginal thickenings of the former separate and divaricate. In peripheral population *B* the apices of these structures are constricted and the marginal thickenings of the epiproct are approximated and subparallel distad. B_1 (Indiana), B_2 (Maryland), and B_3 (west Florida) differ in size and robustness, but are more like each other than any of them is like population *A*. Isophenes may be drawn between the center and periphery of the range approximately as shown, the axis of elongation being along the Appalachian Mountains.

mediacy—in other words, a simple cline affecting a single character. In 1934 Hubbell found that the concealed male genitalia show striking differences from place to place in the range, and two years later Hebard published a revision of *Aptenopedes* based on these and other newly discovered characters. In *sphenarioides* each of the six characters he used was found to vary independently of the others, giving rise to a series of combinations and gradations that are not a linear sequence and are much too complicated to be treated by conventional methods. Hebard strove to apply the geographic subspecies concept to which he was accustomed, and treated the species as follows (Fig. 2); *Aptenopedes sphenarioides apalachee* in southwest Georgia and adjacent Florida and Alabama, with atypical populations *apa-*

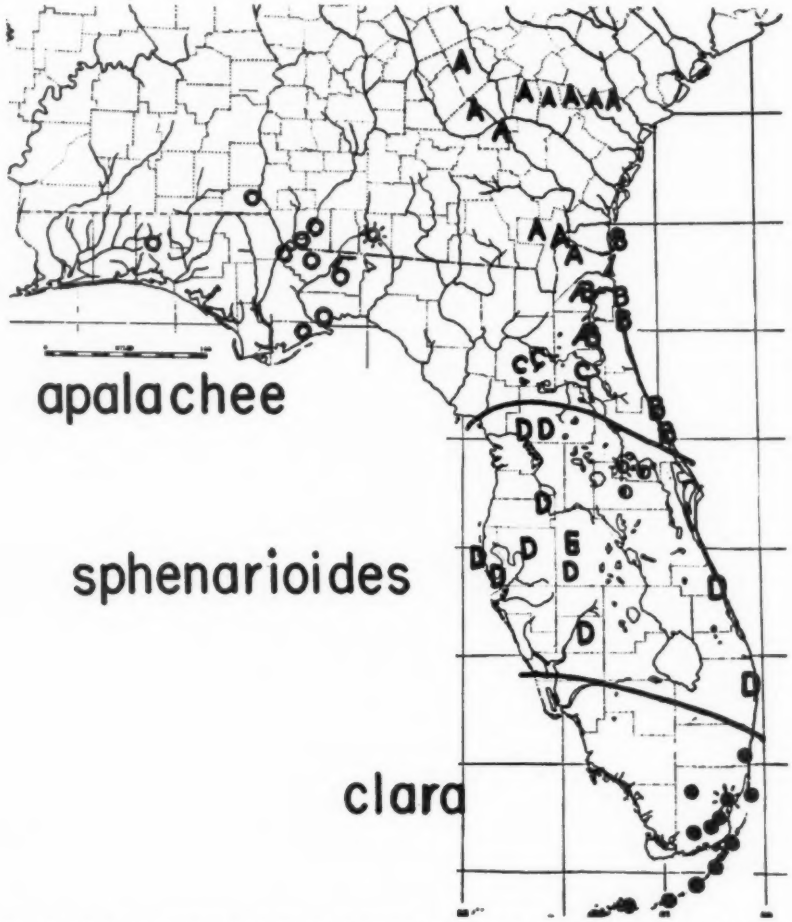

FIG. 2. The subspecies and atypical populations of *Aptenopedes sphenarioides* Scudder, according to Hebard, 1936. The range of the typical form of each subspecies is indicated by an open circle for *apalachee*, a half-filled circle for *sphenarioides*, and a solidly filled circle for *clara*. The atypical populations are indicated by letters, as explained in the text.

lachee A in east central Georgia, *apalachee AB* along the northern St. Johns River, *apalachee B* along the east coast of Florida, and *apalachee C* in the Gainesville region; *A. s. sphenarioides* typical in Seminole and Orange counties, Florida, with atypical populations *sphenarioides D* over most of central Florida and *sphenarioides E* concentrated around Lakeland; and finally *A. s. clara* in the Miami region and southward over the Keys. Analysis of Hebard's data (Fig. 3) shows that each of the eight populations he distinguishes is characterized by a different combination of the variant conditions shown by the six characters he used; some of these characters vary in a clinal fashion while others do not, and no two of them change at the same rates or in the same places. Recent inspection of very much larger series than were studied by Hebard also shows that even greater complexity exists than he suspected. Each additional character considered adds a dimension to the pattern, and there is some indication of the existence of localized ecotypical phases on top of all the other differentiation. As Hebard pointed out, this is an unusually complex situation as seen from the viewpoint of traditional taxonomy; but in the light of the next example it may be interpreted merely as one in which a complexity common in species populations is more easily seen on the morphological level than is usually possible.

Example 4. *Trimerotropis sparsa* (Thomas) (White, 1951, pp. 376–394). This is an oedipodine grasshopper with nearly unbanded hind wings that are pale bluish, greenish, yellowish, or transparent. It has a wide range in arid western North America, extending from Alberta to New Mexico and Arizona, and from North Dakota and Nebraska to Idaho and north-

	Cercus V	Paraproct W	Furcula X	Epiproct Y	Epiphallus Z	Size
apalachee	1	3	X^2	Y^1	1	Small
"A"	2					
"B"	3	1	X^1		2	
"C"						
sphenarioides			X^3	y^1	3	
"D"	4	2	x^1	Y^2	4	Large
"E"		1	X^1		3	
clara	5		x^1		5	

FIG. 3. Non-coincident clinal and other variation in six characters of *Aptenopedes sphenarioides* Scudder, based on an analysis of Hebard's 1936 description of the subspecies and atypical populations. The morphological meaning of the symbols in this table is unimportant for the purposes of this presentation; the significant point is that each added variable character increases the number of possible infraspecific segregates and diminishes the possibility of dealing with the situation in simple nomenclatorial terms.

eastern California. It is chiefly restricted to the so-called shadscale zone, where it occurs especially on dry mud-flats and in eroded badlands. In the eastern part of its range it lives mostly in the river valleys, but in the Great Basin the areas of suitable habitat are extensive. The species tends to occur in small colonies of similar individuals, with considerable differences in size and coloration existing between colonies. White has studied the chromosome complex of *T. sparsa* in populations occurring at 29 localities. He finds that these populations differ in respect to supernumerary chromosomes, chromosomal fusion between autosomes, and structural heterozygosity with respect to acro- and metacentrism in certain chromosome pairs. These are morphological differences, even though they are cryptic and visible only by cytological techniques. Logically they require the same taxonomic consideration as the more easily appreciable differences in average form of a cercus or breadth of a wing-band. White reports that *T. sparsa* is "a species with an extremely complex cytogenetic system, broken up into a number of microgeographic races, each with its own system of cytological polymorphism. . . . [It appears to be a strongly sedentary insect. Differences in cytological composition] may exist between populations less than 20 (and probably less than 10) miles apart which are not separated by any geographic or ecological barrier to the spread of the species." In dealing with the infraspecific entities in *Trimerotropis sparsa*, White treats them as "The Eastern Populations" (Cortez, Cedar Creek, Olathe, Delta, etc.) and "The Great Basin Populations" (Hinckley, White Valley, Cherry Creek, etc.), and shows their differences and similarities by means of graphs. This is the same method used by Dobzhansky and Epling (1944) in dealing with the "chromosome races" of *Drosophila pseudoobscura*, and seems both simple and functional. It permits discussion, grouping, classification, and reference with respect to the subspecific entities being studied, unhampered by the "legalism" and ancient connotations of Linnaean nomenclature. And since this *ad hoc* method, whether it makes use of names, symbols, or graphs, is designed for the treatment of special and particular situations, and for the uses of the small group of workers concerned with those situations, it does not have to be universal or everlasting. The nomenclature adopted for a particular case can be changed or discarded whenever this seems desirable.

Let Freedom Reign

Obviously, everyone is going to deal with infraspecific variation as he feels inclined, since the variety of situations is too great ever to be covered by a set of formal rules. To me, and I am sure to a great many other zoologists, formal nomenclature and its rules are a necessary evil, time spent upon nomenclature is time diverted from the true objectives of our science, and wherever the rules of nomenclature seem unnecessary or inapplicable we welcome the chance to escape their tyranny. The classification and designation of infraspecific segregates seem likely to remain free country for a long time to come. As for myself, I have adopted certain precepts by which to govern my attitudes and actions in this territory. (1) Clinal variation is variation of characters in populations, not of populations. (2) Clines in themselves therefore cannot be taxonomic units. (3) In a population showing only a stepped cline in a single character or in a group of correlated characters it is feasible and may be convenient to treat the segments between steps as subspecies. (4) In populations in which clinal change is gradual or in which two or more non-coincident clines exist it is inadvisable to try to separate subspecies. (5) In general, infraspecific variation is best treated by description, graphic presentation, and non-technical names, not by formal latinized names subject to the rules of nomenclature. (6) Nothing should ever be named for the sake of nam-

ing it, but only in order that something may be said about it.

REFERENCES

BLATCHLEY, W. S. 1920. The Orthoptera of Northeastern America. Indianapolis, Nature Publishing Co.

DOBZHANSKY, TH., and EPLING, C. 1944. Contributions to the genetics, taxonomy and ecology of *Drosophila pseudoobscura* and its relatives. *Carnegie Inst. Wash. Publ.*, No. 554, 1–183.

FULTON, B. B. 1925. Physiological variation in the snowy tree-cricket, *Oecanthus niveus* DeGeer. *Ann. Ent. Soc. Amer., 18*:363–383.

——— 1926. The tree crickets of Oregon. *Oregon Agr. Coll. Expt. Sta. Bull.*, No. 223, 1–20.

——— 1931. A study of the genus *Nemobius* (Orthoptera, Gryllidae). *Ann. Ent. Soc. Amer., 24*:205–237.

——— 1952. Speciation in the field cricket. *Evolution, 6*:283–295.

HEBARD, M. 1934. The Dermaptera and Orthoptera of Illinois. *Illinois Nat. Hist. Surv. Bull., 20*:125–279.

——— 1936. New genera and species of the Melanopli found within the United States and Canada (Orthoptera; Acrididae). Part IV. A revision of the genus *Aptenopedes*. *Trans. Amer. Ent. Soc., 62*:190–222.

HUBBELL, T. H. 1936. A monographic revision of the genus *Ceuthophilus* (Orthoptera, Gryllacrididae, Rhaphidophorinae). *Univ. Florida Publ., Biol. Ser., 2*:1–551.

OLSON, A. L., HUBBELL, T. H., and HOWDEN, H. F. 1954. The burrowing beetles of the genus *Mycotrupes* (Coleoptera: Scarabaeidae: Geotrupinae). *Misc. Pub. Univ. Mich. Mus. Zool.*, No. 84, 1–59.

REHN, J. A. G. 1919. A study of the orthopterous genus *Mermiria*. *Proc. Acad. Nat. Sci. Philadelphia, 71*:55–120.

REHN, J. A. G., and HEBARD, M. 1916. Studies in the Dermaptera and Orthoptera of the coastal plain and piedmont region of the southeastern United States. *Proc. Acad. Nat. Sci. Philadelphia, 68*:87–314.

SABROSKY, C. W. 1940. Entomological usage of subspecific names. *Ent. News, 51*:159–164.

——— 1952. How many insects are there? *In*: Insects. Yearbook of Agriculture, 1952, pp. 1–7. Washington, D. C. (U. S. Dept. Agr.).

WHITE, M. J. D. 1951*a*. A cytological study of wild populations of *Trimerotropis* and *Circotettix* (Orthoptera, Acrididae). II. Racial differentiation in *T. sparsa*. *Genetics, 36*:31–53.

——— 1951*b*. Structural heterozygosity in natural populations of the grasshopper *Trimerotropis sparsa*. *Evolution, 5*:376–394.

The Occurrence of Clines in Molluscan Populations

WILLIAM J. CLENCH

THE selection of a title for this symposium was somewhat unfortunate as it implies that the cline and the subspecies are two opposable entities. The cline is only an orderly or semi-orderly system of change from one complex to another, regardless of whether this is a change from one unit population to another or a gradient between subspecies or possibly even species. On the other hand, subspecies can occur without any "smooth" change or gradient from one to the other, a factor frequently exhibited by insular populations. This often occurs in mollusks where mechanical distribution is perhaps the major means of transport. An appreciation and understanding of the cline as it is interpreted today is not entirely new in malacological studies, though early papers usually refer to this phenomenon as geographic variation. The application of the concept, however, is limited in this phylum to the groups which are more or less sedentary throughout their lives. Except in a very broad way, it would be difficult to apply it to such groups as marine bivalves which have pelagic free-swimming larvae. These larvae may exist in the free-swimming stage for a few hours to more than four weeks, and are thus subject to tidal and oceanic currents which may move them from a few yards to many hundred miles from their point of origin.

Many gastropods are exceedingly localized during their lifetime, the veliger stage being passed within the egg or within the egg capsule, and they remain generally in the locality of their origin. Mechanical dispersal is, however, always possible and, as considered below, a factor of considerable importance in preventing a "smooth" cline.

Before the present subject is developed further, it must be understood that we are still in the fact-finding stage in this phylum. For many species we know little more than the fact that they exist. In addition, lack of collecting leaves tremendous gaps in our knowledge of the distribution of many groups. Undoubtedly when adequate collections are made many species which are now thought to be valid will be found to be connected by a series of transitional forms to others, and thus they will be reduced to subspecies or may even be synonymous with other species. I think that I am safe in saying that we know adequately the life history of about 100 species, a relatively insignificant number out of the more than 100,000 species which have been described in this phylum. Detailed data regarding any one species hardly allow general assumptions for other species even in the same genus.

Marine Forms

As stated previously, most of our marine bivalves and many of the gastropods have free-swimming larvae. Morphologically speaking, the stage at which the young begin their independent existence is probably a minor factor in their development; some are free-swimming from shortly after fertilization, others are retained in the egg or the egg capsule until the late veliger stage, and still others are held captive throughout their larval life. None the less, this single factor in their development affects profoundly their distribution over a given period of time.

Highly localized colonial development is expressed by those species having the last-named type of life history while those with a long larval life are usually uniform throughout their range.

Thais lapillus Linné, the common rock whelk of our New England coast and northern Europe, lays its eggs in small vertical capsules. Some 40 eggs are laid in each capsule, of which only 12 to 14 emerge as young snails. The remainder are "nurse eggs" supplying food for those that hatch. *Thais haemastoma* Linné and its subspecies (Gulf of Mexico and the West Indies) typically produce some 1000 eggs per single capsule, and the young emerge as veliger larvae which are free-swimming for a short period of time and are thus subject to mechanical dispersal by local currents (Clench, 1947). A cline appears to evolve in both these species. In *Thais lapillus* Linné the ratio of colored individuals (those exhibiting orange and dark brown color patterns) to white individuals increases as one progresses from south to north. Even here, factors of ecology may enter the picture. It has been shown that the various types of animals upon which *Thais lapillus* Linné feeds may be responsible for certain of the colorations (Moore, 1936, 1938). However, these ecological studies have been conducted in restricted localities, and have not been applied to the coast as a whole. This species usually feeds upon barnacles and *Mytilus,* and these are the same species at Gloucester, Massachusetts, as they are at Eastport, Maine; yet there are differences in the *Thais,* locally as well as generally from south to north, in the relative abundance of the color forms. The problem needs much more study.

In the area about the Mississippi delta there is found *Thais haemastoma haysae* Clench, a subspecies closely related to *T. haemastoma floridana* Conrad, which exists on both sides of the delta area, i.e., in Mississippi, Alabama, and Florida and again in central Texas. Typical *haysae* is very much larger that *floridana* and, in addition, possesses a double row of large, blunt spines or knobs. It grades into typical *floridana* both east and west of the delta area. It appears that *haysae* is not an ecological form but a genetic element that is partially confined to the many waterways of the vast delta area. Even with a short free-swimming period it exists in an area of very small tidal flow and is thus partially isolated. Elsewhere, as in Texas and in the eastern Gulf along the coast of Alabama and Florida, the interchange of larvae in *floridana* is frequent enough to maintain more or less uniform populations.

Hubendick (1950) has indicated the existence of a cline in *Siphonaria pectinata* Linné, a marine pulmonate of the tropical eastern Atlantic. In these patelliform mollusks, the radial costae increase in number in the various colonies proceeding south from Sénégal to the Guinea coast of Africa.

Studies of our own, now in progress, on the genus *Melongena* of the Florida coast show that certain of the various subspecies in the *corona* complex are connected by a series of transitional populations. This will be discussed in detail in *Johnsonia* (Clench and Turner, 1954, in press).

Freshwater Forms

The cline is perhaps best expressed in mollusks among certain of our freshwater families. A paper by C. C. Adams (1915) on the genus *Io* certainly indicates a well-developed series of clines. In this able report Adams describes some 14 named entities which, in general, show a variation of increased spinosity from the several headwaters downstream in the upper Tennessee River system of Virginia, Tennessee, and Alabama.

The same appears to be true in a study by C. Goodrich (1924) on the genus *Gyrotoma* of the Coosa-Alabama River of central Alabama. Here there is indicated a difference from upstream to downstream in the morphology of shell characters.

No over-all study has been made of the species complex of *Pleurocera undulatum*

Say, a group of rather large snails that are found in the main rivers of the vast Ohio River system. Each major confluent has its own forms, and all seem to merge into one another. Detailed study of this problem would certainly be fruitful.

The three groups mentioned above have been cited only to indicate clines of different complexity: the genus *Gyrotoma,* which is confined to a single river and does not occur in the tributaries; the genus *Io,* which is confined to a single river system and occurs in most of the tributaries; and the *Pleurocera undulatum* complex, which occurs in all the large rivers and tributaries of a major river system. All three groups are in the family Pleuroceridae.

Future study may well indicate that clines are apparent in many species of our freshwater mussels, the Unionidae. This group is complicated exceedingly by many ecological factors, particularly the fact that most species are parasitic for a short or longer period of time on fish, and as a consequence are subject to the distributional eccentricities of their respective hosts.

I seriously question the development of clines among our pulmonate freshwater mollusks. The distributional patterns of these forms appear to be regional; the mollusks occupy small or large geographic areas regardless of river systems, and the lake and pond forms are isolated in much the same way as island populations.

Land Pulmonates

Perhaps the best examples of clines among the land mollusks are to be found in the Hawaiian Islands (Achatinellidae) and the Society Islands (Partulidae). These might be termed microclines as the distance between the extreme points is only a few miles. Both of the above groups are tree snails that live in the valleys and on the ridges of these mountainous islands. In both localities minor changes take place in shell morphology and coloration from one ridge and valley to the next ridge and valley. In the Achatinellidae several clines occur, each with its own specific and subspecific groups. Detailed data on both families are to be had from the studies of Gulick (1905), Crampton (1917 and 1932), and Welch (1938 and 1942).

Certainly, many more and probably quite similar clines occur in several other groups of land snails. However, such monographic studies as have been published were not developed with the cline in mind; they are purely systematic in approach, possibly containing most of the necessary data, but not organized on the basis of geographical or clinal distribution. Such data could be gleaned from the many monographs published by Pilsbry (1889–1935) in the *Manual of Conchology.*

Mechanical transport is a factor of considerable importance in the distribution of land snails. Unquestionably this has added greatly to the problems involved in the study of geographic variation and the development of clines in these groups. Both wind and wave have played their part in distribution. Except for our marine forms with free-swimming pelagic larvae, mollusks are exceedingly sedentary and with few exceptions probably live and die within a few feet or yards of their point of origin. When chance dispersal enters the picture, their distribution may be an orderly sequence but more frequently it is completely haphazard. Such appears to be true of *Liguus,* both in Cuba and Florida. In both areas hurricanes have probably been the most important factor in their dispersal. There are quite definite distributional patterns for many of the color forms, but these cross each other in many directions and do not appear as clines.

Another example of this sort is the genus *Cerion,* a genus of terrestrial and semi-arboreal land pulmonates most abundant in Cuba, the Bahamas, and the Cayman Islands. They occur along the upper strand line that margins the islands, penetrating inland only in the Bahamas where salt spray can still reach them. Here

again, hurricanes play their part in combination with the sea. Storm waves are responsible for carrying these mollusks short or long distances on flotsam. They may even completely destroy a colony in one area and re-establish a few specimens in another some distance removed. It is not at all unusual to find a few dead shells of one species of *Cerion* in a locality now occupied by a totally different species. In other areas two or more apparent "species" may be found along a stretch of coast with an amazing number of hybrid colonies interspersed. I know of no other genus of land mollusks that renders less satisfaction to the taxonomist interested in natural groupings and relationships. It is a genus that should have much interest for the population geneticist, who could make studies under natural field conditions.

REFERENCES

ADAMS, C. C. 1915. The variations and ecological distribution of the snails of the genus Io. *Mem. Nat. Acad. Sci., 12* (2):1–184.

CLENCH, W. J. 1947. The genera Purpura and Thais in the Western Atlantic. *Johnsonia, 2*:61–91.

CRAMPTON, H. E. 1916 [1917]. Studies on the variation, distribution, and evolution of the genus Partula. The species inhabiting Tahiti. *Carnegie Inst. Wash. Publ.*, No. 228, pp. 1–331.

——— 1932. Studies on the variation, distribution, and evolution of the genus Partula. The species inhabiting Moorea. *Carnegie Inst. Wash. Publ.*, No. 410, pp. 1–335.

GOODRICH, C. 1924. The genus Gyrotoma. *Univ. Mich., Mus. Zool., Publ.*, No. 12, pp. 1–32.

GULICK, J. T. 1905. Evolution, racial and habitudinal. *Carnegie Inst. Wash. Publ.*, No. 25, pp. 1–269.

HUBENDICK, B. 1950. Scientific results of the Danish Expedition to the coasts of tropical West Africa 1945–1946. Atlantide Report 1, pp. 151–166.

MOORE, H. B. 1936. The biology of Purpura lapillus. I. Shell variation in relation to environment. *J. Marine Biol. Assoc., 21*:61–89.

——— 1938. The biology of Pupura lapillus. II. Growth. *J. Marine Biol. Assoc., 23*:57–74.

PILSBRY, H. A. 1889–1935. *Manual of Conchology,* Academy Natural Sciences, Philadelphia, series 2, *5–28*.

WELCH, D. A. 1938. Distribution and variation of Achatinella mustelina Mighels in the Waianae Mountains, Oahu. *B. P. Bishop Mus. Bull.*, No. 152, pp. 1–164.

——— 1942. Distribution and variation of the Hawaiian tree snail Achatinella apexfulva Dixon in the Koolan Range, Oahu. *Smithsonian Misc. Coll., 103*, No. 1, pp. 1–236.

The Contribution of Avian Taxonomy

(*Concluded from p. 110*)

LACK, D. 1946. Taxonomy of the robin, *Erithacus rubecula* (Linn.). *Bull. Brit. Orn. Club, 66*:56–65.

——— 1951. Geographical variation in *Erithacus rubecula*. *Ibis, 93*:629–630.

MACKWORTH-PRAED, C. W. 1943. Nature and nomenclature. *Ibis, 85*:223–224.

MAYR, E., and AMADON, D. 1951. A classification of recent birds. *Amer. Mus. Novitates,* No. 1496, 1–42.

MILLER, A. H. 1941. Speciation in the avian genus *Junco*. *Univ. Calif. Publ. Zool., 44*: 173–434.

MOREAU, R. E. 1948. Some recent terms and tendencies in bird taxonomy. *Ibis, 90*:102–111.

SCHLEGEL, H. See Siebold.

SHARPE, R. B. 1909. Hand-list of the genera and species of birds in the British Museum. 5 vols. London.

SIBLEY, C. G. 1950. Species formation in the red-eyed towhees of Mexico. *Univ. Calif. Publ. Zool., 50*:109–194.

SIEBOLD, PH. FR. DE. 1844–1850. Fauna japonica. Aves: TEMMINCK, C. J., and SCHLEGEL, H. Lugduni Batavorum, Apud A. Arnz et socios.

SOUTHERN, H. N. 1946. [Remarks concerning paper by Clancey, *Bull. Brit. Orn. Club, 66*: 86–90.] *Bull. Brit. Orn. Club, 66*:90–92.

TUCKER, B. W. 1946. [Remarks concerning paper by Clancey, *Bull. Brit. Orn. Club, 66*: 86–90.] *Bull. Brit. Orn. Club, 66*:92–96.

WAGSTAFFE, R., and HINCKS, W. D. 1945. Physiological races and nomenclature. *Ibis, 87*: 289–290.

WILSON, E. O., and BROWN, W. L., JR. 1953. The subspecies concept. *Syst. Zool., 2*:97–111.

Summary

J. SPEED ROGERS

IT IS evident that the title "Subspecies *and* Clines" would be more applicable to the ideas presented in this symposium than the antithesis implied by the word *versus*. For at least three of the participants, the central problem is that of the wide qualitative and quantitative variety and range of intraspecific variation versus the fixed nomenclatural status of the subspecies. Perhaps it was this troublesome question of legal nomenclature that suggested that in those situations where it is applicable, the description and plotting of clines would both provide a more accurate picture of geographic variation than arbitrary and poorly limited subspecies, and avoid the concomitant legal erection of more and more trinomials.

There is no dearth of examples, as Burt and others point out, of trinomials having been made for what appear to be arbitrarily selected and poorly defined—probably indefinable—sections of a cline; but as Sibley, Mayr (in letter quoted by Sibley), and Hubbell emphasize, and indeed as Huxley made clear (Huxley, 1942: 206; 226-227), cline and subspecies apply to quite different aspects of variation. As Hubbell puts it, clines apply to characters, not to populations. Nevertheless clines and discernible breaks between adjacent intraspecific populations both involve gene-flow and/or selection and it is to be expected, as Bogert shows, that the geographic and ecological factors of a species' range will, in some instances, result in several marked, concordant clinal changes in zones where a marked check to gene-flow or changes in selection values have created a partial barrier between two parts of a species population. But these appear to be special cases, useful, reassuring, and illuminating when discovered and analyzed, but comparatively rare in the overall problems of systematics. It is also worth noting, as Bogert points out, that the demonstration of such correlations requires an abundance of material and its careful analysis. In most instances clines do not show stepping nor are two or more clines apt to be clearly concordant.

The most apparent consensus of the symposium appears to be that the creation of subspecies is not to be undertaken lightly; that as a legal establisher of trinomials it is not suited for the designation of the huge number of local or other subpopulations that can be discerned in most adequate series of wide-ranging animals; that the trinomial if used at all should attest to the existence of a partially but usually not wholly segregated population of organisms. Few systematists would quarrel with this point of view; its presentation by five competent practitioners in as many fields of systematics comes clearly from the conviction that the subspecies has been decidedly overused and misused. The evidence that a proposed subspecies does represent a partially but usually not wholly segregated population of organisms, maintaining itself in nature, requires both ample data and sound systematic discernment.

As I have re-read the galley proofs of the papers by the members of the symposium, I have come to sense a subtlety not formerly so apparent in Dr. Tate Regan's oft-quoted definition of species: "a community, or a number of related communities, whose distinctly morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them, to a specific name" (Regan, 1926). No provision for more than a most perfunctory and legal competence can be made in any nomenclatural code, and these papers are perhaps most useful in presenting viewpoints

(*Concluded on p. 133*)

After a Century of Darwinism

JOHN L. BROOKS

EVOLUTION AS A PROCESS. Edited by Julian Huxley, A. C. Hardy, and E. B. Ford, with 16 other contributors. London, George Allen & Unwin Ltd., 1954. [Distributed by Macmillan.] 367 pp., illustrated. 25 shillings.

ALMOST a century has passed since Charles Darwin provided the world of thinking men with his compelling accumulation of evidence documenting organic evolution, and promulgated his theory of the importance of natural selection. The appearance of *Evolution as a Process* is an invitation to pause and consider "Darwinism" one hundred years after. The nineteen essays not only provide the reader with the opportunity of examining as many aspects of the processes of evolution but also indicate the general trends of interest in the time since the publication of *The Origin of Species.*

Darwin's work stirred wide interest in the comparative aspects of morphology and embryology. Modern biology rests in large part on the welter of information which accumulated. However, the efforts to systematize this information in accordance with the doctrine of evolution were often speculative far beyond the demands of the observations. The efforts of some of these grand "integrators," who unlike Darwin did not continually subject their beautiful formulations to the crudities of reality, brought down the annoyance and contempt of many biologists upon any interest in systematics, classification, and phylogeny. As so often happens in human affairs, specific excesses provoke generic condemnation.

Fortunately, some zoologists did continue systematic studies with work of the highest calibre through the dark age that ensued. They strove to improve and correct the work of their predecessors. Of these, Garstang, de Beer, and Hadži, along with a small number of others, have managed a revolt against the Haeckelian hypothesis sometimes graced with the appellation "law." A. C. Hardy in his essay, "Escape from Specialization," reviews the development by the late Professor Walter Garstang of the concepts of neoteny and paedomorphosis. These processes by which a successful larval form may become sexually mature and give rise to simplified and well-adapted descendants have probably played a far greater role in animal phylogeny than the majority of biologists appreciate. G. R. de Beer, whose name is closely linked with these new views of ontogeny and phylogeny, has devoted his space in this volume ("The Evolution of the Metazoa") to consideration of Professor Jovan Hadži's views on the origin of the Metazoa, according to which the Platyhelminthes are seen to represent the type of the original Metazoa and the Coelenterata (Cnidaria) and Ctenophora are separate neotenic derivatives of this stock. The amazing similarity of the concepts of neoteny of Garstang and Hadži is another example of that incredible simultaneity of ideas of which the Darwin-Wallace discoveries of the importance of natural selection are a well-known instance. Hadži published his account in Yugoslavia in 1923. Hardy in his essay mentions that the comic verse "Mulleria and the Ctenophore," expressing a similar view of the origin of the Ctenophora, was written by Garstang in 1922 or before, although not published until after his death when Hardy, Garstang's son-in-law, included it in a small volume, *Larval Forms and Other Zoological Verse,* published in 1951.

As Hardy indicates, Garstang's interest in the pelagic larvae of marine invertebrates had early convinced him of the

absurdity of believing that these larvae could possibly represent the adult forms of their ancestors. In the early twenties he led the revolt against the recapitulationists, reminding zoologists of the then century-old statements of von Baer to the effect that an animal may at any stage in its ontogeny diverge from the ancestral course of development. Garstang applied the concept of paedomorphosis to the tunicates in his justly famous paper of 1928. According to his view the tunicates, far from being degenerate chordates, actually retain the sessile habit which likely characterized the ancestral chordate. Their tadpole larvae had developed a locomotor system so efficient that at least one group of modern tunicates has become sexually mature as an enlarged and somewhat modified tadpole. Garstang suggested that a similar step may have been taken by the ancestors of the vertebrates, that a fish (to put it over-crudely) is a modified and oversized tadpole larva which has become sexually mature. As early as 1922 Garstang indicated, again in a comic verse, that Amphioxus might be paedomorphic. Twenty-five years later he developed the idea that Amphioxus was possibly a neotenic derivative of the Cephalaspids, which most probably had an ammocetes larva much like that of modern cyclostomes. This note, which was intended as a letter to *Nature*, was not submitted because he planned to modify it; however, death overtook him before he could do so. Hardy has included the unmodified letter as an appendix. This is primarily of historical interest, since Romer has already indicated this pedigree for Amphioxus. Garstang's elucidation of the origin of at least some of the Siphonophora as paedomorphic derivatives of some hydroid with a floating larval polyp (the actinula) and Gurney's suggestion that copepods are neotenic offshoots of the Decapoda are among the instances which Hardy lists.

Hadži's views on the origin of the Metazoa will be familiar from the summary of his views on phylogeny which recently appeared in SYSTEMATIC ZOOLOGY. G. R. de Beer's essay, "The Evolution of Metazoa," already in press at that time, provides a more detailed account of Hadži's theory that the flatworms developed from primitive infusorians by cellularization, and that the Cnidaria developed from a turbellarian larva that had become fixed by its aboral end and adopted a sessile habit of life. The way in which many details of the biology of these simpler metazoans fall into place in the pattern envisaged by Hadži speaks compellingly in his favor. The insight and hard work which have permitted these workers to achieve an understanding of what have been some of the major steps in the history of animal life merit our admiration and respect.

Some will contend that attempts to unravel the early history of the Metazoa are, and will never be more than, speculation because so much time has passed since the events occurred. However that may be, some events so recent in the history of organic life that they are less than a heartbeat of geological time away have been subject to, if anything, more ill-supported speculation than those most remote. It is understandable and regrettable that self-conscious man may fake fossil remains which purport to be human. It is also understandable and regrettable that reputable students of man's past have been overenthusiastic in their interpretation of man's phylogeny from the fragments of Primate remains which we are so fortunate as to have discovered. It is refreshing and heartening to read a careful and dispassionate analysis of some of the most overspeculated-upon fossils ever to be unearthed. The remains are those of the Australopithecinae and the analysis is done by S. Zuckerman in a contribution entitled "Correlation of Change in the Evolution of Higher Primates."

The fossil evidence of man's evolution must document the acquisition of three of his distinctive bodily attributes: his peculiar brain, his relatively smaller face and teeth, and his upright posture. After

Zuckerman carefully analyzes each class of evidence he concludes that there is no justification for assuming that the brain of the Australopithecinae was like man's, and that their jaws and face show no obvious change toward those characteristic of man. The possible indications of upright posture are more complex. A consideration of the skull indicates that it was balanced on the spinal column as in the apes rather than as in man. The pelvic bones yield no certain evidence of upright posture.

After this judicious evaluation, Zuckerman cautiously states:

> We can safely conclude from the fossil hominoid material now available that in the history of the globe there have been many more species of great ape than just the three which exist to-day. Asia, Africa and Europe were the home of apes of various kinds in the Miocene, Pliocene and Pleistocene. For all that is known about the extent to which the living great apes have diverged from their Miocene forbears, and particularly the extent to which they may have diverged in features of the post-cranial skeleton, it is every bit as likely that some of the Australopithecines represent the forerunners of the modern gorilla and chimpanzee, as that they were the ancestors of some group of protohominids; and far more likely than that, as has been claimed, they were themselves protohominids. (Pp. 348-9.)

Such systematic studies as provide the data of phylogeny have constituted but a small portion of the zoological research of the first half of this century. Genetics, ecology, physiology, animal behavior, biochemistry absorbed the interest of zoologists: the study of evolution in any of its aspects, far from being dominant, was almost viewed with disapprobation.

Genetics, which was later to provide an understanding of the hereditary basis necessary for Darwinian selection, was destined first to provide some of Darwin's detractors with new ammunition. It was not until 1930 that R. A. Fisher in *The Genetical Theory of Natural Selection* pointed out that a particulate theory of inheritance, far from presenting obstacles to Darwinism, actually resolved many of the difficulties which the theory of natural selection caused for Darwin, who considered inheritance to be "blending." Nothing could be more appropriate than that Sir Ronald Fisher write a "Retrospect of the Criticism of the Theory of Natural Selection" for this volume. Included are not only those criticisms which Darwin himself appreciated and attempted to answer but also those brought subsequently.

J. B. S. Haldane is one who along with Fisher, Muller, and Wright has made it clear that slight selective advantages, too small to be detected in one generation, could over long periods of time produce the remarkable, so often incredible, results of organic evolution. The fact that evolution appears static during the lifetime of any observer—although in actuality it may now be proceeding at an almost unprecedented speed—must indicate that the forces causing evolution are almost in equilibrium. The bulk of Haldane's essay, "The Statics of Evolution," is concerned with the answers which have been given to the question of why, selection being as intense as we know it usually is, heritable variation does exist within any population. Why do deleterious mutants persist in natural populations? Haemophiliacs have only about a quarter of the chance of normal persons to leave offspring, yet haemophilia has persisted, albeit as a rarity, for two thousand years. In evaluating the factors which may act to secure the continued presence of these mutants, Haldane's "own very tentative opinion is that heterosis will be found to be the main cause of genetic variation within most species." He goes on to say:

> If the views here stated are true, much of the rather speculative human biology which passes under the name of eugenics will turn out to be incorrect. Various types of human being, such as giants, dwarfs, idiots, saints, mathematicians, murderers, and musical composers, are rare, and there is evidence that, in a given social background, membership of each of these classes is to some extent genetically determined. The innate endowments needed in a first-rate musician or mathematician are obviously rare. We should like to make them common. It is doubtful whether

such an attempt is likely to succeed until we know how rare they are in fact, and still more why they are so rare. Part of the reason is almost certainly that exceptional genotypes are relatively infertile. This does not mean that natural selection is so altering populations that they are becoming rarer (though this is, of course, a possibility). It seems to me that the best provisional hypothesis is that populations are nearly in stable equilibrium as regards the genes concerned. If so we have less to fear from the sterility of highly endowed types and less to hope from eugenics than has often been thought. (P. 117.)

Haldane makes a brief mention of the possibility suggested by Sewall Wright that in small populations all alleles but one may be lost by chance. This genetic drift or the "Sewall Wright effect" has been the center of the most recent of selection-antiselection controversies. While Haldane suggests that there may be some evidence in its favor, Sheppard concludes his "Evolution in Bisexually Reproducing Organisms" with the statement: "Thus Wright's concept of drift, though frequently invoked as an important agent in evolution, must be judged of negligible significance as compared with selection." This conclusion is reached after a survey of the results of field studies on the genetics of populations including those which he and Cain have done on the snail *Cepaea*.

E. B. Ford, whose name together with that of R. A. Fisher leaps to mind as being antithetic to Wright's, writes on "Problems in the Evolution of Geographical Races." In connection with Ford's consideration of clines, polymorphism, and races, H. N. Southern's fascinating account of "Mimicry in Cuckoos' Eggs" might well be read with profit. Southern sees the gens (that part of a cuckoo population which parasitizes one species of host) as intermediate in stability between polymorphs and races. After a careful examination of recent experimental and observational data, Ford concludes that there are three main kinds of results of the adaptation of a species. Where its range is wide, and pertinent aspects of the environment change progressively, clines will result. Here he considers that mere distance may permit genetic differences to accumulate, and this may lead to the formation of subspecies. Where the environment of a large habitat varies but in a geographically irregular pattern, the communities are apt to be remarkably similar. This situation Ford considers the least likely to exhibit evolutionary change. When the habitat is such that the population consists of small, more or less isolated communities, each will rapidly become adapted to its own peculiar environment. These smaller populations may be dissimilar when compared with each other and with any larger, more uniform population, suggesting that "drift" may have occurred. Ford has investigated such a situation among some Scilly Isles butterfly populations, and finds that the "small" populations are too large for drift to have occurred. However, the fact that an isolated population has achieved a large size does not mean that the founding colony was necessarily of comparable size.

E. Mayr ("Change of Genetic Environment and Evolution") is also concerned with the divergence of relatively small, peripherally isolated populations when compared with the larger populations occupying a more or less continuous range. He cites the example of a Papuan kingfisher which has three very similar subspecies on the mainland of New Guinea, but with five of the six populations on small, adjacent islands so different that they have been described as separate species; four are still so regarded. This situation is a familiar one to systematics and I venture to say that most who read this speculative essay will, with the reviewer, find it most stimulating. Mayr feels that neither "drift" nor selective adaptation to the different environment is sufficient to account for the striking divergences characteristic of these isolated populations. His hypothesis, overbriefly stated, says that the selective value of a gene when it occurs only in combination with the necessarily limited gene pool of a

founding colony may be very different from its value when imbedded in the genetic environment of a large, continuous population.

Such a genetically depauperate population might flourish best in an environment comparatively free of predators and competitors. Certainly the archipelagoes and ancient lakes attest to the evolutionary success which such populations may enjoy. Mayr suggests that some of the bursts of new types with which the paleontologist is often confronted might be similar in nature. Enough of the peculiar elements of Lake Baikal have spread into the Yenisei River so that the fauna of this river has a facies different from that of other Siberian rivers. Should this association ever be able to spread to these adjacent freshwaters, it is possible that a faunal replacement could occur which would appear to a future paleontologist much as such past replacements appear to our contemporaries.

There are few glimpses of evolution on the grand scale in this volume. The only contribution from paleontology is "Mountain Revolutions and Organic Evolution." In this, T. S. Westoll expresses his skepticism of any more or less direct control of the course of evolution by earth movements. He concludes:

> . . . There is a dynamic interplay between living organisms and their environments, so much is certain. But crustal unrest of itself is not enough; what matters is specific changes in specific environments which are either fully occupied by, or become available to, forms of life suitably fitted to inhabit them. It may well be that restriction of an environment may lead to great extinctions; but it is rarely possible to take into account all (or even most of) the factors involved in such extinctions. . . . Great evolutionary developments almost inevitably involve successful exploitation of new opportunities; similar *conditions* may well have occurred many times, but creatures fitted for such an adventure may rarely be available to break in and deploy widely. (P. 262.)

Hardy and Mayr have made suggestions as to how new opportunities might be exploited. Mayr closes with mention of the Hawaiian dragonfly, which E. Zimmerman has described, the larva of which has forsaken the watery habitat of its ancestor for the moist humus and plant debris of the forest floor. What if it should now become neotenic!

Because the color of insects and birds has done much to call them to man's attention, it comes as something of a surprise (at least to this reviewer) to realize that the Primates are the only placental mammals able to perceive it. Conversely, the gaudy buttocks of drills and baboons are among the few bright spots that mammals exhibit. E. N. Willmer's absorbing essay ("Color Vision and Its Evolution in the Vertebrates") is full of information about the occurrence, sensory basis, and biological significance of color perception. The correlations between the presence of color, the behavior associated with its possession, and the ability of animals in the role of mate, rival, or enemy to perceive it, are also considered in the contributions of H. B. Cott ("Allaesthic Selection and Its Evolutionary Aspect") and N. Tinbergen ("The Origin and Evolution of Courtship and Threat Display"). Huxley in 1938 proposed that the term "allaesthetic" be used for characters "which exert their biological effect via the distance receptors of another individual, i.e., those of smell, hearing and sight." Cott has ably integrated the vast, scattered information on visual characters and their biological significance. Tinbergen's account of these displays in the stickleback, but especially in birds, supplements and develops one aspect of allaesthetic selection.

The fact that a successful animal must mate, feed, and escape being eaten, to mention only the basic biological interactions, requires that its coloration and/or behavior associated with any one of these aspects of existence cannot be too deleterious to the others. Natural selection achieves the niceties of balance which so often claim our wonder. This variety of behavior is most evident among birds, and James Fisher is mainly concerned with

showing that all these kinds of behavior manifest the sociality of birds, a fact appreciated by few biologists, even those working with them ("Evolution and Bird Sociality"). Although the colorful aspects of birds attract much attention and study, D. Lack would have us remember that birds are subject to selection for characters such as reproductive rate, just as are creatures as little social as plankton crustacea. "The Evolution of Reproductive Rates" gleans information from many groups of animals to support the thesis that under the influence of natural selection a species will tend to lay the number of eggs which will provide the greatest surviving progeny.

The appreciation of color display depends upon much more than the possession of a sense organ composed of elements which have a differential spectral response. The central connections responsible for the interpretation of the patterns of stimuli are just as important and even more difficult to study. Two of the essays approach, along different avenues, the problems of central nervous systems. Bernhard Rensch is interested in the effect of size on function in vertebrate brains, while J. Z. Young suggests that information theory may help us to understand the biological significance of neural memory and heredity, which he conceives as memory derived from ancestors. "The Relation between the Evolution of Central Nervous Functions and the Body Size of Animals" is a summary of much able work and would seem to indicate a more fruitful approach than that of "Memory, Heredity and Information." Rensch and his co-workers have compared related species of mammals of different size with regard to the cytoarchitecture of their brains and their ability to learn. From the investigations of comparative structure, Rensch provisionally generalizes that the larger species in comparison to a smaller related one has an absolutely larger brain and forebrain; a relative enlargement of the progressive regions of the cortex; and usually more and absolutely larger ganglion cells with, therefore, more dendrites. In the learning experiments the smaller species was usually better at learning simple tasks, while the larger one solved more complex problems more easily and retained the learning longer. These researches offer hope of much greater understanding of the evolution of the functioning of the vertebrate brain.

That color, with its roles in various animal interactions, should be mentioned in the contributions bearing on the evolutionary aspects of animal ecology and behavior is not surprising. That color should have much to do with plant evolution was surprising to this reviewer. Of course the correlated evolution of the structure of flowers and the insects which pollinate them has long been appreciated. But in the evolution of forest trees red is the important color and insects cannot see red. Some primitive trees of tropical forests have large capsules which open to display conspicuous red fruit, and thereby hangs a tale. Indeed, the tale told in "The Evolution of Tropical Forest" is as engrossing as a first-rate suspense novel and far more satisfying intellectually.

E. J. H. Corner dubs this the "durian theory," and in it envisions the interactions of plants and animals in creating the bewildering complexity of the tropical forest:

> While all these changes have been wrought upon the forest so as to render the results at first sight unconnected, one reflex persisted. A stimulus to the repast for birds and primates, at least, has been the colour of the fruit. On redness their eyes have feasted: with blackness they have been frightened. Redness is attractive and stimulant: with green, it is gay; but the combination with black becomes diabolical, long after the horrors and delights of the forest have been forgotten. It may seem a far cry from a tomato to a sunrise, or from a durian to a petticoat, but redness in human experience seems referable to the dim origin or durianism. (P. 45.)

Evolution as a Process calls to mind *The New Systematics*. As in that earlier collection, the high quality of the contributions is enviable. It is almost certain

that this work will prove equally stimulating to students of systematics and evolution. And as in that work the introductory essay is an able summary by Julian Huxley. The title of the book reflects Dr. Huxley's expression in "The Evolutionary Process" that biologists in the last two decades "have paid increasing attention to clarifying the *process* of evolution, as opposed to, or in addition to, analysing its *mechanism*." His evaluation of the trends of evolutionary studies and his assessment of their present status are made from the vantage point of a leader. His essay should be encountered as written, not in summary. The necessity of reference throughout the book to clines, allaesthetic selection, relative growth—all terms and concepts which Huxley introduced—testifies to the diversity of his interests and the penetration of his insight. His co-contributors join, on the occasion of his sixty-fifth birthday, in expressing, as a foreword to this volume, their appreciation of his services to biology. That this issue of SYSTEMATIC ZOOLOGY should report a symposium on the current application of the "cline" concept is appropriate; may it also express in part our appreciation to Julian Huxley, and to the man whose ideas two Huxleys have courageously defended and developed.

Subspecies and Clines: Summary

(*Concluded from p. 126*)

that merit consideration in forming the systematist's necessarily subjective judgment of what is systematic competence.

A more adequate summary would present some account of the discussion from the floor, but neither my memory nor my notes are adequate. Perhaps the chief tenor of this discussion was a defense of the place of the subspecies in systematics, its value in stating relationships, and its important use for island taxa and those which replace each other geographically. Perhaps the nearest thing to a common thread which I perceived in this discussion is colored by my own opinion that the subspecies is most useful as a synthesizing concept, much less useful in analysis, and that its usefulness is, at least in part, a function of the completeness of the available data.

REFERENCES

HUXLEY, J. S. 1942. Evolution: the modern synthesis. Harper and Brothers, New York.

REGAN, C. T. 1926. Presidential address, Sect. D, Rept. Brit. Assoc. Adv. Sci., 75-86.

The Problem in Oyster Taxonomy

GORDON GUNTER

HEDGPETH (1954) has resurrected an old question concerning oyster taxonomy and evolution which has not been alive since the days of d'Orbigny. It was settled by Leymerie (1840, 1874) a hundred years ago, although he was not fully vindicated until some fifteen years ago. Nevertheless, lest biologists not acquainted with oyster taxonomy be led astray, I must take up the pen and reply. The points upon which the argument rests seem to be two.

1. Oysters from four different zones of the Jurassic (Liassic) show gradations from the ordinary oyster shape to the extreme ramshorn upward curl of the beak of *Gryphaea,* and these populations may be arranged in a statistical series with intermediate stages being most numerous.

2. There exists a ramshorn specimen of the Japanese oyster, *Crassostrea gigas,* of which a photograph is shown, and Packard (1923) found an Eocene specimen of *"Ostrea"* of the *Exogyra* type (lower valve laterally curved).

From this, Hedgpeth suggests that factors "which induced the *Gryphaea* lines, are still latent in the estuarine stock of oysters" (p. 24) and says "the names we choose to apply to our modern stocks of oysters may be more a matter of taste (and predisposition) than a reflection of genetic circumstances." He then suggests that *Gryphaea* be retained for both the Mesozoic fossils and the living group, as originally used by Lamarck. This suggestion imaginatively propounds confusion, and the whole argument is untenable. One small fact has been skillfully arrayed against a vast mass of contrary evidence, most of which was not mentioned.

In the early days of taxonomy it was common to confuse unrelated species. Lamarck did not separate the fossil *Gryphaea* from the living *Crassostrea* and indeed it was only on the basis of fairly recent knowledge that the latter genus was clearly separated from *Ostrea* (cf. Gunter, 1950). A similar instance was Walbaum's inclusion of the paddlefish, *Polyodon,* with the sharks. There are hundreds of others. Hedgpeth would have us return to this early stage of taxonomic knowledge of the oysters.

Within certain limits, defined by the fact that the shells consist of two hinged valves, oysters are among the most plastic organisms known. They vary in all sorts of ways within those limits, a fact attested by many workers. The writer once found one shaped like Cinderella's glass slipper and sent it off to Washington. Nelson (1938) called attention to a specimen which was mistaken for *Spondylus* by a worker familiar with the latter group. He also said that certain shells of the Virginia oyster in his collection came well within the range of five other species, which belong to two genera. Ranson (1942) said the distinction of a genus based upon sculpture of the shell is artificial. The writer (1950, p. 438) said, "It is difficult to separate genera and exceedingly difficult to separate species of oysters on the basis of shell characteristics alone." Incidentally, some paleontologists have stepped into this pitfall. I once saw, in a well-known museum, a group of fossil oysters which had not been fully separated from their matrix and were obviously a block from one reef. They showed only the variations exhibited by many single species. Yet they had been carefully divided into seven species and were so labeled. Thus, in no group of animals is there more taxonomic necessity for using full statistical series, adequate to show the wide variations, than in oysters. The writer (Gunter, 1950) previously sug-

gested that oyster taxonomists would have to emulate fishery biologists and analyze large volumes of data before variations of the species are properly understood. Statistical analyses have been adopted in taxonomic studies of several animal groups and would be particularly appropriate for oysters. An approach to oyster taxonomy with this point of view would preclude overemphasis of rare and freakish specimens. Shell characteristics may be of considerable taxonomic value when properly evaluated. For example Thomson (1954) carefully discussed and made good use of these "conchological" characters in his examination of the taxonomic status of Australian oysters.

Lamarck was followed by Deshayes and later by d'Orbigny, who stood against the erection of the genera *Gryphaea* and *Exogyra* on the grounds that exogyroid and gryphoid oysters and ostreiform Gryphaeas and Exogyras are found. When Leymerie gave his final paper before La Société Géologique de France, P. Fischer remarked that among the Portuguese oysters at Arcachons a small part were similar to Exogyra and a few were similar to Gryphaea. These similarities were of course faint. Thus Hedgpeth's example is not new, so far as significance goes, although previous examples are largely fossil, and we have only to carry his idea a little further to arrive at the conclusion that *Gryphaea, Crassostrea,* and *Exogyra,* too, are congeneric. That is out of the question. Some of the fossil species were huge and in the living state must have weighed fifty pounds. In comparison present species are pygmies. Size is not a good final difference, but merely an indication. There are others. Jourdy (1924) wondered why such eminent paleontologists as Deshayes and d'Orbigny would insist upon relating fossil and living oysters in the face of Leymerie's (1840, 1874) clear exposition of the differences of three groups, which Jourdy summarized as follows:

1. The Oysters, of which the beak is not twisted in an involute spiral, which possess neither lobe nor keel on the lower valve.

2. The Gryphaeas, of which the beak is not twisted in an involute spiral and is raised directly over the upper valve, with a lateral lobe ridging most often the lower valve.

3. The Exogyras, of which the lower valve is keeled, deep, and terminated by a recurved beak in an involute spiral to one side of the shell.

Jourdy also pointed out that the ligament of *Exogyra* is radically different in that one of the lateral ligamental areas is suppressed. This is a definitive character.

Leymerie ably defended the separation of *Gryphaea, Exogyra,* and modern oysters (*Ostrea,* now known to consist of two genera) against his better-known colleagues, Deshayes and d'Orbigny, for a matter of forty years, his last paper being delivered when he was eighty-four years old. His ideas were finally adopted. They were based upon shell characteristics, and since these are notoriously poor for differentiation of oysters, the wonder is that he was so essentially correct, as was shown later by other means. The answer seems to be that, taking variations into account, he took a broad view and saw the situation in its true light.

Jourdy discussed polymorphism in the Exogyras, which in some cases led to the appearance of characters similar to *Gryphaea, Pycnodonte,* and *Alectryonia,* and said that it was attained by several different species during the Mesozoic and was thus a *collective* character of the genus. He added that it was an example of *convergence* and that very similar polymorphism was later assumed by the chamids. Nelson (1938) pointed out the importance of the promyal chamber in modern oysters of the *Crassostrea* group, and its use as a character separating them from *Ostrea.* This and other characteristics of the soft parts usually leave paleontologists cold, because they are of no use in fossil studies. However, Nelson pointed out that the promyal chamber, which essentially is an extension of the epibran-

chial chamber lying between the mouth and the muscle, is present only in those oysters with the muscle placed far posteriorly. Thus the promyal chamber is correlated with placement of the muscle scar, which can be used by paleontologists. He further stated that placement of this scar in both the fossils, *Gryphaea* and *Exogyra,* indicates that they had no promyal chamber. This is another definitive point favoring Leymerie's original interpretation.

The crowning definitive work was carried out by Ranson, who applied studies of prodissoconch shells of the larvae to problems of oyster taxonomy, following the lead of Bernard (1898) who initiated studies of the larval shells of lamellibranchs. Ranson (1939, 1942, 1948) showed by descriptions, drawings, and photographs that morphology of the prodissoconch shells of living oysters affords clear differentiation between species within a genus and also between genera. Owing to the fortunate fact that these little shells remain attached to the beak of the resulting oyster, Ranson also recovered them from numerous fossils. He has shown that the prodissoconch of the ancient *Gryphaea* (*Liogryphaea*) was equivalve, while that of *Crassostrea* (*Gryphaea*) is inequivalve. The larval shells of *Exogyra* are also equivalve but differ from *Gryphaea* in other ways. These discoveries are definitive with respect to generic differentiation of oysters and they set the whole matter to rest. Thus prior work stands as sufficient refutation of Hedgpeth's contentions, but certain details of his remarks should be answered.

Contrary to his supposition that the ramshorn *Gryphaea*-like modern specimens may not be rare, it can be stated unequivocally that they are extremely rare and his is the only one known. If this character had any genetic fixity strong enough to relate the living genus to one of 60 million years ago, it would certainly not exist in only one species of living oysters but would also be found in other species of the same genus. However, I have handled thousands and seen hundreds of thousands of *Crassostrea virginica* with never a ramshorn oyster. Furthermore, if the farfetched supposition that "we may be on the threshold of a new outbreak" of such forms were correct, it would not modify the situation because his figured specimen is not similar to the ancient *Gryphaea* as defined, except in one respect, and falls within Leymerie's "Huîtres," i.e. living oysters.

Living oysters possess a hook or beak of the lower shell. It may be straight or slightly curved to the right or upwards, faintly similar to *Exogrya* or *Gryphaea,* but it may even curve downward, similar to neither. To take the whole group, the beak of oysters may be short and straight or long and curved, and the longer the beak the greater the tendency to curve. In two fossil groups there was a strong tendency for the curves to go laterally and be involute or to go upward but not involuted. The short-beaked fossils superficially resemble living oysters, and living oysters resemble them, because it is a family characteristic for oysters to have beaks. The relation is not necessarily closer than the one that all oysters have a peculiar and distinctive ostreiform shell. The crux of the situation may be stated as follows: In fossil oysters of the *Gryphaea* and *Exogyra* types there was a strong tendency for the shells to end in a long, curved beak, and millions of individuals exhibited this character, although there occurred some short-beaked specimens which may have been largely young ones. On the other hand all living oysters (millions or billions of them) have short beaks, except for one known specimen. On a numerical or statistical basis the ratio is infinitesimally small.

Geneticists have come to the conclusion that certain genes for fur color of quite unrelated mammals, such as mice and guinea pigs, horses and cattle and others may be the same. But these are certainly fixed and recurring. Thus any similar long-standing gene for ramshorn shells in oysters would not necessarily demonstrate

generic fixity or identity, and the resulting phenotype would certainly occur fairly often in any case. Hedgpeth's argument is based upon the discovery of one ramshorn oyster among millions living. It is very rare and no taxonomist would think of including the ramshorn curl as a generic characteristic of *Crassostrea*. If this is an adequate base for congeners, what weight do we give to the forward movement along the jaw of new teeth, and replacement of worn-out ones, in the elephants and manatees? This is a stable, fixed character among these dissimilar beasts and it is quite unique among mammals. It is clear that unique characters may be shared by widely different groups.

The ramshorn Japanese oyster is an interesting oddity, if only because of extreme rarity, but to base a claim of congenerism between living oysters and Mesozoic fossils upon that alone, is basing far too much upon far too little.

The Mesozoic oysters were a diverse, widespread group with many giant species. They died out as many other things did at the end of that period. The present species have changed little during the Cenozoic, as Ranson (1951) has stated. The genera of the family Ostreidae have been fairly adequately delineated on the basis of a great deal of morphological evidence, which is not likely to be greatly changed in the future. And, as I have previously stated, "*Gryphaea* cannot be accepted for any (of the three) living genera of oysters," under the present rules (see also Hertlein, 1933, Stenzel, 1947, and Thomson, 1954). The main question in oyster taxonomy at present is whether we will make an exception to the rules and apply Lamarck's *Gryphaea* to a living genus and *Liogryphaea* to the fossils, thus interjecting great confusion into the literature, especially paleontological literature, or follow the rules and apply Lamarck's *Gryphaea* to fossils and *Crassostrea* to a living genus. This question is purely man-made and it has no bearing upon the generic differences of oysters, which are now well substantiated.

REFERENCES

BERNARD, P. 1898. Recherches ontogéniques et morphologiques sur la coquille des Lamellibranches. *Annales Sci. Nat., Zool., 8*:1–208.

GUNTER, G. 1950. The generic status of living oysters and the scientific name of the common American species. *Amer. Midl. Nat., 43*:438–439.

HEDGPETH, J. W. 1954. A problem in oyster taxonomy. *Syst. Zool., 3*:21–25, 45.

HERTLEIN, L. G. 1933. A new gryphaeoid oyster from the Eocene of California. *Trans. San Diego Soc. Nat. Hist., 7*:227–278.

JOURDY, E. 1924. Histoire naturelle des Exogyres. *Annales Paleont., 13*:1–104.

LEYMERIE, M. 1840. Thèse sur les caractères distinctif des Huîtres, des Gryphées et des Exogyres. (Not seen.)

——— 1874. Sur la necessité de conserve, au moins sens le rapport géologique, les Gryphées et les Exogyres. *Bull. Soc. Géol. France, 3rd. ser., 2*:141–145.

NELSON, T. C. 1938. The feeding mechanism of the oyster. I. On the pallium and the branchial chambers of Ostrea virginica, O. edulis, and O. angulata, with comparisons with other species of the genus. *J. Morph., 63*:1–61.

PACKARD, E. L. 1923. An aberrant oyster from the Oregon Eocene. *Univ. Oregon Publ., 2*, No. 4, 1–15.

RANSON, G. 1939. Le provinculum de la prodissoconque de quelques Ostréides. *Bull. Mus. Nat. d'Hist. Natur., 2nd. ser., 11*:318–332.

——— 1942. Note sur la classification des Ostréides. *Bull. Soc. Géol. France, 5th ser., 12*:161–164.

——— 1948. Prodissoconques et classification des Ostréides vivants. *Bull. Mus. Roy. d'Hist. Natur. Belgique, 24*, No. 42, 1–12.

——— 1951. Les Huîtres. Biologie-Culture. Lechevalier, Paris.

STENZEL, H. B. 1947. Nomenclatural synopsis of supraspecific groups of the Family Ostreidae (Pelecypoda, Mollusca). *J. Paleontol., 21*:165–185.

THOMSON, J. M. 1954. The genera of oysters and the Australian species. *Austral. J. Mar. and Freshwater Res., 5*:133–168.

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Points of View

Formulation of Locality Data

In the earlier days of this continent's development, collectors and naturalists frequently labelled their material as coming from such places as "Californie," "Indian Territory," or "Mexico." Sometimes, although the localities were more explicitly stated, they marked the headquarters of the collector or the point from which shipment to a distant museum was made. All too often such places were hundreds or even thousands of miles from the point of collection. Indeed, cases can be cited in which specimens are labelled as having come from a continent other than that on which they were actually collected. The difficulties resulting from such poor records are apparent to all who try to work with them. Collectors have, during this century, generally provided more adequate and precise locality data. During the early decades, designating the collection site by the name of the nearest town was adequate for the purposes of systematic zoology at that time, namely, species description and distribution.

With the change of emphasis from the species level to that of the subspecies and more recently to the local population level, such data have become less and less adequate. Every modern student who has attempted to make a large-scale map showing the distribution of collection sites of an organism is painfully aware of the frustrating difficulties involved. These difficulties arise almost entirely from the inadequacy with which a locality is pinpointed. The need for good locality data is glaringly apparent, for our systematics is expressed largely in terms of morphologic variation, and variation is often expressed in terms of its geographic distribution. Hence, our systematics can be no more precise than our locality data.

This paper constitutes a plea to the collector of animals to take enough care in the formulation of locality data to make sure that his specimens will be useful to future workers. It is directed primarily to vertebrate zoologists, but with minor modifications the plan suggested can apply to all fields of biology.

I have frequently heard a poorly recorded locality defended on the basis that a better record or an interpretation of the data is contained in the collector's field notes; or again, that one wastes too much time in devising a detailed set of data. Neither objection is valid. Field notes are only rarely available to future workers who may not even know such notes exist. And as all who have attempted to plot localities on a map know, many more hours are spent trying to locate a poorly designated collection site than are minutes saved by the collector in providing ill-chosen data.

There is no single good way in which to record localities. I offer only a general pattern which must be modified by sound judgement to suit the case in hand. But first, I would point out various widely used practices and present reasons why they might profitably be avoided.

The identification of a collection site by the arbitrary system of coordinates known as township, range, and section would approach an ideal system were it not for the fact that most often maps with such coordinates are not readily available to workers for all the areas needed. Also, the system is limited to only parts of the United States. Used to supplement the more conventional locality data these data are useful and desirable.

Use of impermanent reference points is a poor investment of time and effort. A

good reference point should be readily identifiable at any time in the future. In this era of rapid change the problem cannot always be readily solved. However, it should be obvious that road junctions, wayside taverns, highway numbers, campgrounds, and small ponds are ridiculously transitory features which even twenty-five years from now will likely be renamed, moved, or eliminated. Some collectors maintain that one should avoid man-made reference points whenever possible, for they are notoriously temporary.

To use "speedometer" or road mileages in lieu of airline miles is frequently an expedient but also an inexcusably careless method of indicating distances. When an unqualified mileage is given one assumes that it is airline. Too often, road mileages are not qualified as such, and in mountainous terrain especially, such data can lead to gross errors in interpretation. Furthermore, when plotting localities from road mileages, wide variations are apparent depending on the scale of the reference map used and on the grossness of its details. Finally, of least immediate importance but still worthy of consideration is the fact that many highway distances are being changed yearly because of rerouting, straightening of old roads, and the construction of new, more direct ones. Probably few road-mileage distances recorded today can be used with any real confidence twenty years hence.

It should be a matter of course for the collector to use as reference points *only* those features which are shown on ordinary small-scale maps. At the collection site a local name or topographic feature may seem thoroughly adequate, whereas in reality the name appears on no published map or on only very special or large-scale ones. National parks and monuments and other recreational areas are especially rich in such strictly local names. One can always find good points of reference to which the local names or features should be made subordinate.

Maps are usually provided with some sort of horizontal and vertical overprinted grid. This makes it easy to estimate with considerable accuracy cardinal compass directions from any point on the map or even the primary subcardinal directions. However, further subdivisions, such as SSW or ENE, are difficult to estimate accurately enough, especially when the distance from the reference point is not short. It is better to indicate distance and direction in terms of cardinal compass points only, "so many miles N, so many E."

Elevation is a useful adjunct to other locality data, especially in regions of diverse topography. However, the use of elevation alone as a reference point is to be avoided. Only rarely does a subsequent user of the data have topographic maps of all necessary areas at hand.

In my experience the most useful locality data include the following items, all of which should be included whenever possible or pertinent, even when they are inconvenient to determine.

1. *Country.* This is usually used only in the case of foreign materials.
2. *State* or equivalent.
3. *County* or equivalent. This is extremely useful in restricting the search for a specific point.
4. *Local area,* e.g. valley, mountain, lake, river, etc., when such is a prominent feature.
5. *Distance* and *direction* in airline miles from a restricted and *permanent* reference point. Generally a town or mountain peak is satisfactory enough if it appears on common small-scale maps. If the name of a town is identical with a nearby mountain, lake, or river, insert the word town in parentheses, thus, "Boulder Creek (town)."
6. *Elevation.* Normally this can only be expressed to within 50–100 feet. If measured by an instrument uncorrected for barometric changes or if estimated, it should be qualified as "approximate."
7. *Date of collection.*
8. *Collector.*
9. *Field number* if notes are recorded for the specimen or the collection site.

10. Additional data are often desirable or even required depending on the type of material collected. Sex; gonad, embryo, or ovum size; age; weight; certain standard measurements; stomach contents; parasites; color of soft parts; ecological association or habitat, and weather conditions are often included on the locality tag. Information on which of these additional data to include for any particular group of animals is best obtained from specialists on that group or from handbooks on collecting.

If such a procedure is followed our collections will be more useful to contemporary workers and will be more likely to remain useful in the future. Furthermore, our efforts will be greatly appreciated not only by the contemporary worker but also by workers of future generations, for collections cannot be remade every hundred years or so. Even more important, many areas will in a few years' time be so changed by man's activities as to alter the fauna irretrievably.

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Stability in Taxonomy

Disapproval of adjustments in scientific names, valid or invalid, has been a source of continual differences among systematists so that some species have received considerable attention, attention which has sometimes added chaos to the already established confusion. The taxonomist has often, without justification, been unmercifully criticized for changing, adding, coining new names, and re-establishing or attempting to re-establish the use of older names.

Hedgpeth in the March issue of SYSTEMATIC ZOOLOGY for the current year, discusses "A Problem in Oyster Taxonomy." Apparently the main purpose of his discussion is to establish the proper generic name of the commercial oyster found on the eastern coast of North America. For many years this form has been recognized as *Ostrea virginica* Gmelin. The generic name of the oyster in question is not one of priority or of use, but one of accuracy. As time progresses and new zoological information is available, it is necessary to readjust our nomenclatorial concepts in keeping with such advances, for as Mayr (1954) has stated, "Every addition to our zoological knowledge may result in a revision of classification and a subsequent alteration of the binomen."

The original scheme of classification as everyone knows, was based on morphology, but that has not sufficed because of the recognition that genetic, physiological, and ecological factors modify and play an essential part in the evolutionary and subsequent natural relationships of organisms. Mayr (1954) has said that the stability of the binomen depends on the finality of zoological classification on the generic level.

Let us first consider some examples of this lack of stability in the Mollusca. The commercial oyster has been variously assigned to each of the three genera: *Ostrea, Gryphaea,* and *Crassostrea.* It is no longer acceptable to utilize the shell alone as the sole character for identification of members of this phylum. As pointed out by Gunter (1950), the paleontologists alone have the right to use only part of an animal, such as the shell, to describe a species, and even they have more difficulty in relating fossil forms to modern species and genera than in relating the living groups to one another, on the shell character exclusively. The similarity of the shells of the fossil and Recent species is recognizable as evidence of relationship only when the shells are compared and examined in series. Abbott (1954) states that *Gryphaea* should be reserved for fossil forms only.

Without using generic designations, it has been found that by considering char-

acters other than the shell, two types of living oysters have evolved (Orton, 1928). Gunter (1950) gives an excellent summary of these findings and differences in structure, larvae, etc., and these will not be repeated here. Shell characteristics of pelecypods which are of taxonomic importance include form of beak, hinge margin, sculpture of inner margin of valves, particularly at the hinge and immediately on either side of it, and form and position of the muscle scars (McLean, 1941). As for the other differences in the two types of living oysters, Type 1 and Type 2 respectively, one is larviporous, one is not; one lacks a promyal chamber, the other has one; one is hermaphroditic, the other is of one sex; one spawns at medium-low temperature (15°C.), the other at moderately high temperature (20°C.); one flourishes in temperate regions, the other in tropical and subtropical regions (Gunter, 1950). It has been shown that the spawning temperature is not as definitive as was once believed. Orton (1928) wrote that Type 1 was largely marine and lived in a more stable environment than Type 2, which was subjected to and better adapted to changes in turbidity, temperature, and salinity.

Our commercial oyster of the East Coast was assigned to Type 2, and Orton (1928) suggested that these two types be given generic or subgeneric rank. Sacco made the American species *virginica* the genotype for *Crassostrea* (Sacco, 1897), and it was subsequently given subgeneric rank by some investigators. Since obviously *O. lurida* and *O. edulis,* representatives of Type 1, and *O. virginica* and *O. angulata* of Type 2, are certainly distinctive, it appears that *Ostrea* should be confined to Type 1 as originally suggested by Orton (1928) and that *Crassostrea* then be used for Type 2, and *Gryphaea* remain for the Jurassic and Cretaceous fossils. Those individuals who are familiar with oysters seem to prefer *Crassostrea,* but its status is for the systematist to decide. The commercial oyster still has a scientific name which is unresolved, and whichever genus is used is the one preferred by the current investigator.

The oyster is not the only common animal about whose proper scientific name there is a lack of unanimity. The commercial hard clam or quahog, formerly *Venus mercenaria,* was given subspecific recognition as *Venus mercenaria mercenaria* and *Venus mercenaria Mortoni.* A majority of modern workers eliminated this generic name, and the so-called northern quahog and the southern quahog have become *Mercenaria mercenaria* and *Mercenaria campechiensis,* respectively. Consequently Venus is used as a common name, not as a genus for American shells, thus *Mercenaria* Schumacher 1817 takes its place (Abbott, 1954).

The Atlantic ribbed mussel, originally *Volsella demissa* (Dillwyn), was later placed in the genus *Modiolus,* Lamarck 1799, but because of the Rule of Priority, *Volsella,* Scopoli 1777 was again used. Attempts have been made to suppress *Volsella* because *Modiolus* had been so widely used (Baily, 1951; Cox, 1951). By the time this was submitted for consideration to the International Commission of Zoological Nomenclature, *Volsella* was again becoming prominent in the literature.

The southern, oyster, beaked, hooked, or curved mussel, *Brachidontes recurvus* (Rafinesque) was placed in the genus *Mytilus,* but this has been found to be in error as the animal fitted the genus description of *Brachidontes* as described by Swainson in 1840, which he designated as having numerous small teeth at the hinge.

From this discussion, it becomes apparent that the common names of animals are more stable in time than are the scientific names. The common names are, however, neither as precise nor as universal as the scientific names. Despite this fact, it has been suggested that common names might be more useful than scientific names because of their greater stability and less frequent change. Even with common names we find great variation in different parts of the country, for some are local in their use, and some even designate dif-

ferent animals. Several such common names have been mentioned previously but other examples include the maninose for the soft-shell clam; the horse mussel and the ribbed mussel for members of the same genus; the black mussel, blue mussel, or edible mussel for *Mytilus edulis*. The term gopher in one area means a snake, in another a rodent, and in a third locality, a turtle.

Solutions to purely nomenclatorial problems are based on arbitrary decisions. That these decisions are codified in the International Rules of Zoological Nomenclature and that they are based on so-called principles such as the Law of Priority make them no less arbitrary. Since animals do not have names until they are designated by man, names will continue to change in a somewhat arbitrary manner. Even the establishment of Official Lists, and the suspension of Rules to maintain stability, will not avoid purely nomenclatorial changes; they may, in fact, result in more changes, as happened in the case of *Squilla empusa*.

The genus name *Squilla* was first used by Fabricius in 1787, and it was unquestioned until Rathbun in 1899 and again in 1902 reported that *Squilla* as used for a decapod crustacean was a junior homonym of *Squilla* as used for a genus of amphipods. She pointed out that the oldest available name for the genus in question was *Chloridella* Miers 1880. Actually, among fifteen papers published on the genus since 1902, there are only four in which *Chloridella* has been substituted for *Squilla*, despite the recommendation of Miss Rathbun. However, the name *Chloridella* was widely used in this country, as evidenced by the fact that the generic name *Chloridella* is used in Pratt (1935) where *Squilla* is given as a synonym. Bigelow in 1931 applied to the Commission for a suspension of Rules in order to preserve *Squilla* for the decapod, since it had become fixed in the literature. In 1945, the Commission granted Bigelow's request and the name *Squilla* was retained (Opinion 186). However, the common name "mantis shrimp" survived unchanged.

It is important that systematists appreciate the difficulties which any arbitrary system imposes. The entire purpose of these comments is to emphasize the following and concluding statement which was made to the author by Dr. G. W. Wharton, Head, Department of Zoology, University of Maryland. *Common names change from place to place; scientific names from time to time.*

ABBOTT, R. T. 1954. American seashells. Van Nostrand, New York.

BAILY, J. L. 1951. Proposed use of the plenary powers to validate the generic name *Modiolus*, Lamarck 1799, supressing the generic name *Volsella*, Scopoli 1777 (Class Pelecypoda) and matters incidental there-to. *Bull. Zool. Nomencl., 6*:61–71.

COX, L. R. 1951. Support of Mr. Joshua L. Baily's proposal that the plenary powers should be used to supress the generic name *Volsella*, Scopoli 1777 for the purpose of validating the generic name *Modiolus*, Lamarck 1799 (Class Pelecypoda). *Bull. Zool. Nomencl., 6*:71–72.

GUNTER, G. 1950. The generic status of living oysters and the scientific name of the common American species. *Amer. Midl. Nat., 43*:438–447.

HEDGPETH, J. W. 1954. A problem in oyster taxonomy. *Syst. Zool., 3*:21–25.

MAYR, E. 1954. Notes on nomenclature and classification. *Syst. Zool., 3*:86–89.

MCLEAN, R. A. 1941. The oysters of the western Atlantic. *Acad. Nat. Sci. Philadelphia, Notulae Naturae, 67*:1–14.

International Commission of Zoological Nomenclature. 1945. Opinion 186, Suspension of the rules for *Squilla* Fabricius (J. C.) 1787 (Class Crustacea, Order Stomatopoda). Opinions and Declarations 3, Part 5:53–64.

ORTON, J. H. 1928. The dominant species of *Ostrea*. *Nature, 121*:320–321.

PRATT, H. S. 1935. A manual of the common invertebrate animals. Blakiston, Philadelphia.

SWAINSON, W. 1840. A treatise on malacology or natural classification of shells and shellfish. London.

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Punch-Card Taxonomy

Editor,

SYSTEMATIC ZOOLOGY:

In reading the article "The Construction of Keys" by Z. P. Metcalf in the March issue of SYSTEMATIC ZOOLOGY, I noted that a very useful but not commonly known type of key was not covered. This is a key which is put on punch cards.

In practice, one tabulates the characters which one thinks are useful key characters. These characters are then checked on all available specimens and a code devised to cover these characters. Then a punch card is made out for each species and the coded data punched out on each card.

There are many advantages in using this type of key. (1) If a part of the specimen to be keyed is missing, the specimen can usually still be determined. (2) If a specimen has any peculiarities, all of the species having this character can be immediately selected. (3) Where one alternative of a dichotomy is difficult to select, this character can usually be skipped entirely. (4) New species are added to the key by merely adding a new card. If new characters are used, these characters may be added to all of the older cards. (5) The characters used to separate a specimen may be utilized in any order desired. (6) Keys to be published may be readily made up from the cards; the making of tentative keys and their revising as new data are added is obviated. (7) The card for a given species gives a ready summary of all relevant characters for that species.

The main disadvantage of this type of key is that it is time-consuming to make up. Generally, it can be done only by a specialist in a particular field. Also, the key cannot easily be published. However, as a research tool, this type of key is, in the experience of the author, unexcelled.

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Editor,

SYSTEMATIC ZOOLOGY:

A preliminary meeting was held recently to explore the possibility or advisability of developing a uniform system for use in coding biological taxonomic entities. Participants at this exploratory meeting were from the Library of Congress, the U. S. Department of Agriculture, the Smithsonian Institution, and the Chemical-Biological Coordination Center.

It is known that several laboratories are entering the results of their experiments on machine or hand-sort punch cards and that at least a few are listing the species of plants or animals tested, by means of a code on these punch cards. In order to facilitate the exchange of information between various laboratories, it would seem to be highly desirable for these research groups to use a uniform taxonomy coding system. If the need or usefulness of uniformity is confirmed by sufficient biologists, a start on the formation of a standardized code should be made as soon as possible so that the conversion from individual codes can be accomplished with a minimum of effort.

The interested persons who have been informally discussing the project do not want to set plans in motion for the actual codification unless there is a real or potential need for it. Our immediate problem, therefore, is to determine what areas of biology could be usefully served by a standard taxonomic code. We are, therefore, requesting that those who have worked out or adopted a system for coding taxonomic entities, or who may be conducting work which might benefit from such codification, submit their opinions concerning a standardized biological taxonomy code.

Letters should be addressed to:

G. CONGDON WOOD
Chemical-Biological Coordination Center
National Research Council
2101 Constitution Ave., N. W.
Washington 25, D. C.

People and Projects

The Society of Systematic Zoology participated in the meeting of biological societies sponsored by the American Institute of Biological Sciences at Gainesville, Florida, on September 5-9. The Society's program included a session for contributed papers and joint sponsorship with the Society for the Study of Evolution and the American Society of Ichthyologists and Herpetologists of a symposium entitled "The Origin and Evolution of the Biota of Florida." A. S. Romer, R. A. Howard and T. H. Hubbell participated in this symposium over which K. P. Schmidt presided.

The roster of contributed papers is as follows:

Blackwelder, R. E. and Hoyme, L. E., U. S. National Museum, Washington, D. C. Statistics, Experiment, and the Future of Biology.

Meglitsch, Paul A., Drake University, Des Moines, Iowa. Non-morphological Traits in the Taxonomy of Myxosporidia.

Young, Frank N., Indiana University, Bloomington, Ind. The Problem of Subspecific Variation in Aquatic Coleoptera.

Peters, James A., Brown University, Providence, Rhode Island. A Proposed Method of Bringing the 10th Edition of the *Systema Naturae* up to Date.

Wallace, H. K., University of Florida, Gainesville, Florida. Variations in *Phidippus audax* (Hentz). (Aranae, Salticidae).

A new edition of the *Classification of Insects* by Brues, Melander, and Carpenter has just been published as Bulletin 108 of the Museum of Comparative Zoology, Harvard University. The new edition, which contains 917 pages and 1219 figures, includes a new section devoted to the extinct orders and families of insects. The keys to the families of the Lepidoptera, both adults and larvae, have been entirely revised by C. L. Remington; and K. Christiansen has revised the key to the Collembola. Bound copies of the volume may be purchased from the Museum of Comparative Zoology for $9.00 each; no unbound copies are available.

Permanent headquarters for the George Vanderbilt Foundation, a newly formed scientific research organization, have been established at the Natural History Museum of Stanford University. Ichthyologists of both the University and the Foundation expect to benefit greatly from their collaboration in research work. Stanford has been a center for fish studies since the days of its first president, David Starr Jordan, one of the world's great ichthyologists. The University's collection of more than half a million fishes, which he began, is one of the finest in existence. It is surpassed in variety only by the great national collections in Washington, Paris, and London.

Several expeditions for collecting Pacific Ocean fishes have been sponsored in the last three years by George Vanderbilt of Honolulu, some of them jointly with government agencies. These field trips have already produced notable collections of South Pacific fishes, gathered in the vicinity of the Hawaiian, Tuamotu, Society, Leeward, Line, and Caroline islands. Plans for the Foundation were laid on the first expedition to Polynesia by Vanderbilt, himself an accomplished scientist and explorer, and three companions: Vernon E. Brock, head of Hawaii's Department of Fish and Game; Dr. Earl S. Herald, curator of the Steinhart Aquarium in San Francisco; and Dr. Robert R. Harry, then assistant curator of fishes at the Academy of Natural Sciences of Philadelphia. All are Stanford graduates. The initial task of the Foundation, the four decided, should be to gather urgently needed information about the fishes of the South Pacific, and make it available through publication.

SYSTEMATIC ZOOLOGY is published quarterly by the Society of Systematic Zoology. Its purpose is threefold: To publish, and therefore to encourage the preparation of, contributions on basic aspects of all fields of systematics, principles and problems; to provide a suitable forum for discussion of the problems of the systematist and his methods; and to report as news the other activities of the Society of Systematic Zoology.

Contributions of the following types are solicited: Papers on principles and the applications of principles of wide implication and general interest in any phase of systematics, such as comparative anatomy, zoogeography, paleontology, taxonomy, classification, evolution, or genetics; discussions of methods, specific problems, and activities of systematists; discussions of new books and monographs; and news of systematists, organizations interested in systematics, research and teaching programs, expeditions, collections, meetings, and anything else of interest to systematists.

Consult recent issues for the style to be followed in the preparation of manuscripts. Contributors are encouraged to submit line drawings and diagrams to illustrate their articles. Half-tones may be accepted where necessary to the article.